Shell and ligament microstructure of selected Silurian and Recent palaeotaxodonts (Mollusca: Bivalvia)

Joseph G. Carter

Department of Geological Sciences, University of North Carolina at Chapel Hill, North Carolina 27599-3315, U. S. A.

Abstract: Silurian *Praenucula faba* Liljedahl, 1994, had a nacroprismatic shell and a submarginal, simple, amphidetic ligament with a posterior, lamellar/fibrous component and an anterior, lamellar component. Praenuculids are suitable ancestors for both nacroprismatic nuculids such as *Nuculoidea pinguis* (Lindström, 1880), and nacroprismatic "ctenodontids" such as *Tancrediopsis gotlandica* (Soot-Ryen, 1964). Nuculids evolved by shortening and submerging the posterior part of their ancestral simple ligament to make an internal resilium, whereas solemyoids, including "ctenodontids", elevated the posterior part of their ancestral simple ligament to make a parivincular ligament. Judging from Silurian *Tancrediopsis*, "ctenodontids" were morphologically, microstructurally, and ligamentally well suited for ancestry to the Solemyoidea. Within the Silurian-Recent family Nuculidae, the Nuculominae Maxwell, 1988 retained largely nacreous shells without denticular composite prisms; the Nuculinae Gray, 1824, retained largely nacreous shells but evolved denticular composite prisms; and the Palaeonuculinae *subfam. nov.* evolved largely porcelaneous shells without denticular composite prisms. Palaeonuculines differ from pristiglomid nuculoideans in retaining traces of ancestral laminar structure in the form of matted structure or early juvenile nacre.

The family Cardiolariidae Cope, 1997 is characterized primarily by anterior palaeotaxodont or pseudotaxodont hinge teeth that are abruptly enlarged relative to posterior palaeotaxodont teeth, and by the plesiomorphic absence of a resilium. Although the Silurian cardiolariid *Ekstadia tricarinata* Soot-Ryen, 1964 is porcelaneous, earlier cardiolariids may have been nacreous.

The presence of at least minor amounts of large tablet, imbricated nacre in Early Cambrian *Anabarella* Vostokova, 1962, *Watsonella* Grabau, 1900, *Pojetaia runnegari* Jell, 1980, and *Fordilla troyensis* Barrande, 1881 indicates that this feature is plesiomorphic for the Bivalvia rather than synapomorphic for "fordilloids". As a paraphyletic grade, "fordilloids" document the evolutionary transition in shell and ligament microstructure from laterally compressed monoplacophorans to crown group bivalves.

Key Words: Bivalvia, Palaeotaxodonta, ligaments, shell microstructure, evolution, Palaeonuculinae

The Palaeotaxodonta Korobkov, 1954, is an ancient subclass of medium-size to minute, equivalve, marine bivalves characterized by test-cell larvae, a deeply cleft foot with papillate edges, palp proboscides, distinctive stomach anatomy, and the lack of a crystalline style (Waller, 1998). Palaeotaxodonts are also characterized by particular patterns of pedal and adductor musculature, and variably developed or secondarily reduced palaeotaxodont hinge teeth (Carter *et al.*, 2000). Shell microstructure in the subclass Palaeotaxodonta has long been recognized as convergent on other bivalves, but it is nevertheless important for defining palaeotaxodont families and subfamilies (Douvillé, 1913; Schenck, 1934; Taylor *et al.*, 1969; Maxwell, 1988; Carter, 1990). The shell microstructures in this subclass are richly varied, with outer layers ranging from homogeneous to fibrous prismatic, simple prismatic, spherulitic prismatic, dissected crossed prismatic, and denticular composite prismatic, and middle and inner layers ranging from nacreous to homogeneous, matted, crossed acicular, simple crossed lamellar, and complex crossed lamellar (Bøggild, 1930; Taylor *et al.*, 1969; Carter, 1990;

among others). The superfamilies Nuculoidea Gray, 1824, Nuculanoidea Adams and Adams, 1858, and Solemyoidea Gray, 1840 each include nacreous and non-nacreous taxa, with nacre representing the ancestral middle and inner layer microstructure (Douvillé, 1913; Taylor, 1973; Carter, 1990). Palaeotaxodont ligaments are similarly diverse, with an ancestral dorsal, simple ligament supplemented evolutionarily by a resilium in certain nuculoids and nuculanoids, or modified into a parivincular ligament in solemyoids. The resilia may be fully mineralized or only laterally mineralized, and their mineralization may be fibrous and/or granular (Waller, 1990; Carter, 1990).

Very little is known about early palaeotaxodont shell and ligament microstructure. Published accounts of pre-Devonian palaeotaxodont microstructure are limited to observations of relict nacre in Ordovician *Palaeoconcha* sp. (Mutvei, 1983), and *Deceptrix levata* (Hall, 1847) (Carter *et al.*, 1990a:303). Microstructural relicts have also been described for Cambrian *Pojetaia* Jell, 1980, and *Fordilla* Barrande, 1881 (Runnegar, 1983, 1985; Runnegar and Bentley, 1983; Runnegar and Pojeta, 1985, 1992; Geyer

and Streng, 1998), but these "fordilloids" remain controversial with regard to their relationship with crown group bivalves (see discussion, below).

The present paper describes the shell and ligament microstructure of four Upper Silurian palaeotaxodonts from the Mulde Formation of Gotland, Sweden, and three Recent palaeotaxodonts. These are the first descriptions of shell and ligament microstructure for a cardiolariid, praenuculid, "ctenodontid," and pristiglomid, and for a Recent member of the nuculid subfamily Palaeonuculinae *nov.*

The taxonomic arrangement of this paper follows the phylogenetic classification by Carter *et al.* (in press), but with inclusion of the family Pristiglomidae Sanders and Allen, 1973 in the superfamily Nuculoidea, and with subdivision of the Nuculidae into three subfamilies.

MATERIALS AND METHODS

Specimens of Recent *Pristigloma nitens* (Jeffreys, 1876) were provided by Dr. John A. Allen of the University Marine Biological Station, Millport, Isle of Cumbrae, Scotland. Topotype specimens of Recent *Condylonucula maya* Moore, 1977, were donated by the late Dr. Donald R. Moore. The loan of Silurian palaeotaxodonts from Gotland was arranged by Ingela Chef-Holmberg of the Swedish Museum of Natural History, Stockholm. Most of the Silurian Gotland specimens came from the Wenlockian, Upper Silurian Mulde Formation near Djupvik. Some of the Silurian specimens lacked detailed locality information, but their color and preservation suggest this same provenance. The geologic and stratigraphic setting of the Mulde Formation has been described by Kershaw (1993) and Munnecke *et al.* (1999). The Silurian fossils are now deposited at the Swedish Museum of Natural History, Box 50007, S-104 05, Stockholm, Sweden (RMMo). The Recent nuculoideans are deposited at the Yale University Peabody Museum of Natural History (YPM).

The methods of microstructure analysis follow Carter and Ambrose (1989). The terminology of shell and ligament microstructure is based on Waller (1990), Carter (1990), and Carter *et al.* (1990b). Abbreviations in the text and figures are:

> ALL: anterior lamellar ligament
> CA: crossed acicular
> CCL: complex crossed lamellar
> CL: (simple) crossed lamellar
> FCCL: fine complex crossed lamellar
> FL: fibrous ligament
> Fo: fossette
> HOM: homogeneous
> ICCL: irregular complex crossed lamellar
> N: nacreous

> P: prismatic
> PFL: posterior fibrous ligament
> RMMo: Swedish Museum of Natural History, Stockholm
> UNC: University of North Carolina at Chapel Hill
> YPM: Yale Peabody Museum

MICROSTRUCTURAL PRESERVATION

Bivalves from the Upper Silurian Mulde Formation are preserved in a manner similar to those described by Carter and Tevesz (1978a, 1978b) and Carter (1990) from the Middle Devonian Hamilton Group near Morrisville, New York. Relict shell and ligament microstructures are visible in acetate peels of diagenetic replacement calcite, even though fracture surfaces and x-ray diffraction give no indication of preserved aragonite. This preservation differs from that described by Sandberg and Hudson (1983) for Jurassic calcite-replaced bivalves, where some original aragonite is still present. Microstructural relicts in the Silurian shells probably reflect differential etching rates induced by organic matrices. Darker colored specimens are commonly better preserved than lighter colored ones, suggesting that reducing conditions have favored the retention of this matrix. All presently examined Silurian bivalves were originally aragonitic, based on their microstructures and uniform alteration to calcite.

Studying relict shell and ligament microstructure commonly requires multiple sections through the same shell, and in some instances the examination of several shells to obtain adequate information for every shell layer. The excellent relict preservation of some of the present Silurian shells can be illustrated by comparing acetate peels of Carboniferous, nacroprismatic nuculids and polidevciids with original aragonite (Fig. 1.1, 1.2), with acetate peels of Silurian, nacroprismatic *Praenucula* and *Tancrediopsis* with recrystallized shells (Fig. 1.3, 1.4). Finely prismatic, crossed acicular, and fine complex crossed lamellar structures in a modern malletiid (Fig. 2.1-2.3) can similarly be compared with the same microstructures in Silurian *Ekstadia* (Figs. 2.4, 2.5).

The present descriptions of relict ligaments are based on dorsoventral, serial sections through united valves, supplemented by Liljedahl's (1994) excellent illustrations of prepared hinges and ligament insertion areas. Mineralized ligament sublayers are generally well preserved in the Mulde bivalves (Figs. 1.5, 1.6). The former presence of lamellar ligament can be inferred from localized concentrations of framboidal pyrite. However, caution must be exercised in doing so, because pyrite can also be concentrated in other enclosed or semi-enclosed spaces influenced by the reducing chemistry of tissue
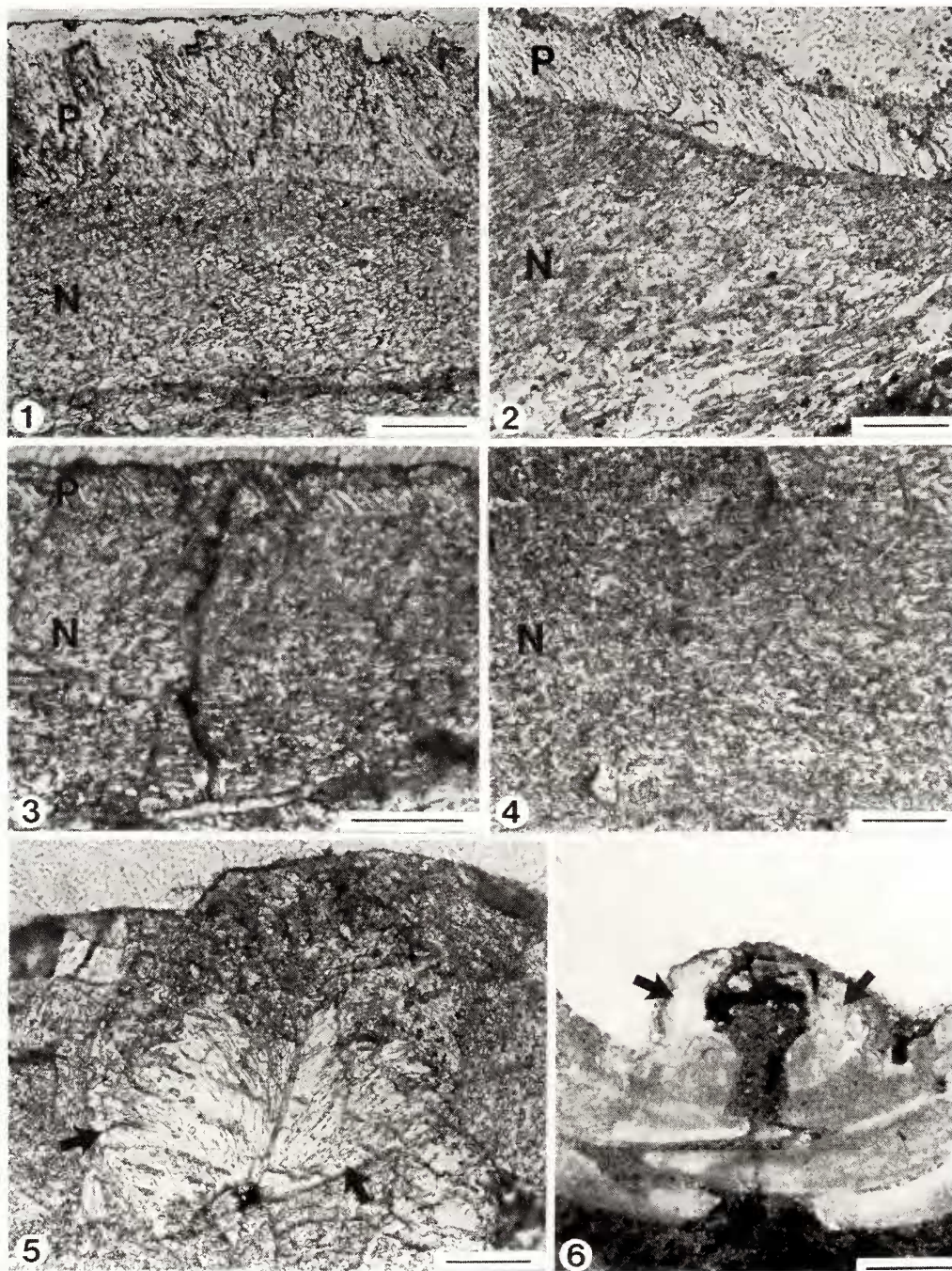
Fig. 1. Acetate peels of dorsoventral sections through Silurian and Carboniferous palaeotaxodonts, showing prismatic outer layers (P), nacre (N), and fibrous ligament (at arrows); shell exterior is up in all figures; the ventral shell margin is toward the right in 1.1-1.3; bar scales = 50 μm in 1.1-1.5, 500 μm in 1.6. 1.1, radial, ventral section through the prismatic outer and nacreous middle layers of Upper Carboniferous *Nuculopsis girtyi* Schenck, 1934, Magoffin Member of Breathitt Formation, Daniel Boone Parkway near Hazard, Kentucky, UNC 7357; original shell aragonite is preserved. 1.2, radial, ventral section through the prismatic outer and nacreous middle shell layers of Upper Carboniferous *Phestia bellistriata* (Stevens, 1858), Kendrick Shale Member of Breathitt Formation, Floyd County, Kentucky, UNC 13649; original aragonite is preserved. 1.3, radial, ventral section through Upper Silurian *Praenucula faba* Liljedahl, 1994, Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15908, showing relict prismatic outer and nacreous middle shell layers. 1.4, relict nacreous laminae in the umbonal inner shell layer of Upper Silurian *Tancrediopsis gotlandica* (Soot-Ryen, 1964), Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15768. 1.5, relict ligament fibers in the submarginal, simple ligament of Upper Silurian *Ekstadia tricarinata* Soot-Ryen, 1964, Mulde Formation, Djupvik, Gotland, Sweden, RMMo 15469; the fibrous ligament is flanked by porcelaneous structure, here poorly preserved, and is overlain by a concentration of framboidal pyrite that suggests the former presence of lamellar ligament. 1.6, transverse section through the parivincular ligament and hinge of *T. gotlandica*.

decomposition. Lamellar ligament is presently inferred to have been present only if pyrite is localized in a position compatible with the presence of ligament, *e.g.*, between submarginal fossettes or internal resilifers, and if the pyrite is significantly more concentrated than in adjacent restricted spaces. For example, framboidal pyrite is highly concentrated between the resilifers of *Nuculoidea pinguis* (Lindström, 1880), but not within its adjacent shell interior (Fig. 6.6). On the other hand, the anterior, submarginal fossettes in *Tancrediopsis gotlandica* (Soot-Ryen, 1964) do not provide unequivocal evidence for lamellar ligament because their pyrite is only slightly more concentrated than between the adjacent hinge teeth (Fig. 9.5). Relict lamellar ligament in a dorsal, submarginal fossette cannot be differentiated from overlying relict periostracum. However, dorsal, submarginal fossettes in modern palaeotaxodonts are either non-ligamental, in which case the periostracum, if it spans the valves, generally does not descend deeply within the fossette, or they are ligamental, in which case the fossette is filled primarily by lamellar and perhaps also fibrous ligament, with relatively little periostracum deposited within the fossette.

OBSERVATIONS OF SHELL AND LIGAMENT MICROSTRUCTURE

Subclass Palaeotaxodonta Korobkov, 1954

Carter *et al.* (2000) divided the subclass Palaeotaxodonta into the monophyletic superorders Nuculaniformii Adams and Adams, 1858, and Nuculiformii Gray, 1824. The Nuculiformii shows a basal dichotomy between *Eritropis* Pojeta and Gilbert-Tomlinson, 1977, and the rest of the superorder, followed by a dichotomy between the Cardiolariidae Cope, 1997, and an unnamed clade in which the Tironuculidae Babin, 1982, Praenuculidae McAlester, 1969, and the clade of Nuculoida plus Solemyoida differentiate in that sequence. Within the Solemyoida, *Tancrediopsis* Beushausen, 1895, is basal to the clade of *Ctenodonta* Salter, 1852 plus Solemyoidea Gray, 1840.

Superorder Nuculiformii Gray, 1824
Family Cardiolariidae Cope, 1997

Cope (1997:736) provided the following diagnosis for the Cardiolariidae: "Palaeotaxodonts with separate anterior and posterior dentitions, in which the hinge lies along line of posterior teeth; anterior teeth, which may be enlarged, lie below hinge axis. Ligament external, opisthodetic." External, opisthodetic ligaments and ventrally positioned, anterior hinge teeth are not, however, unique to the Cardiolariidae. These two features also characterize certain praenuculids, such as *Palaeoconcha* Miller, 1889, and

Similodonta Soot-Ryen, 1964. The cardiolariids *Cardiolaria beirensis* (Sharpe, 1853) and *Praeleda subtilis* Cope, 1999, have anterior hinge teeth that differ from the typical palaeotaxodont pattern in number and/or arrangement, but this is similarly not diagnostic of their family. The cardiolariids *Praeleda costae* (Sharpe, 1853), and *Deceptrix carinata* Fuchs, 1919 have more typical anterior, palaeotaxodont hinge teeth (see Cope, 1997, text-fig. 3). Based on the phylogenetic analysis in Carter *et al.* (2000), a more appropriate diagnosis for the Cardiolariidae is the presence of anterior palaeotaxodont or pseudotaxodont hinge teeth abruptly enlarged relative to posterior palaeotaxodont hinge teeth, *i. e.*, "heterotaxodonty", and the plesiomorphic retention of an opisthodetic, simple ligament without a resilium.

Soot-Ryen (1964:502) placed *Ekstadia* in the family Ctenodontidae, whereas Liljedahl (1994) transferred it to the nuculanoidean family Malletiidae Adams and Adams, 1858, largely on the basis of its pallial sinus. *Ekstadia tricarinata* Soot-Ryen, 1964 resembles *Cardiolaria beirensis* and *Praeleda subtilis* in having a heterotaxodont hinge, an opisthodetic, simple ligament, and no resilium. It also resembles *P. compar* (Barrande, 1881) in having a pallial sinus (Pfab, 1934, pl. 3, fig. 7). On the basis of these similarities, Carter *et al.* (2000) placed *Ekstadia* in the Cardiolariidae.

Except for possible relict nacre in Ordovician *Deceptrix levata* (Hall, 1847) (Carter *et al.*, 1990a:303), cardiolariid shell microstructure has not previously been described.

Ekstadia tricarinata Soot-Ryen, 1964 (Figs. 1.5, 2.4, 2.5, 3, 4)

Liljedahl (1994) reported that *Ekstadia* has an external, opisthodetic ligament. However, the "nymph" that he illustrated for *Ekstadia kellyi* Liljedahl, 1994, (his fig. 34K) is the margin of a fossette for a submarginal, simple ligament. The present observations of *E. tricarinata* are based on ten dorsoventral sections and two anteroventral, commarginal to oblique sections through a pair of valves 8.2 mm in length (RMMo 15469; Fig. 3.7), and five dorsoventral sections and the anterior part of one anteroposterior section through a second pair of valves, also 8.2 mm in length (RMMo 15468).

The ligament is simple and opisthodetic, with a planar to slightly arched, fibrous sublayer inserting into rounded to V-shaped (in cross section), submarginal fossettes (Figs. 1.5, 3.2-3.6, 4.5). The fossettes extend anteriorly only as far as the beaks (Fig. 4.5). The fibrous portion of the ligament is thick in comparison with the hinge, and extends continuously between the valves (Figs. 1.5, 3.2-3.6). Concentrations of framboidal pyrite are compatible with the former presence of lamellar ligament in the dorsal part of
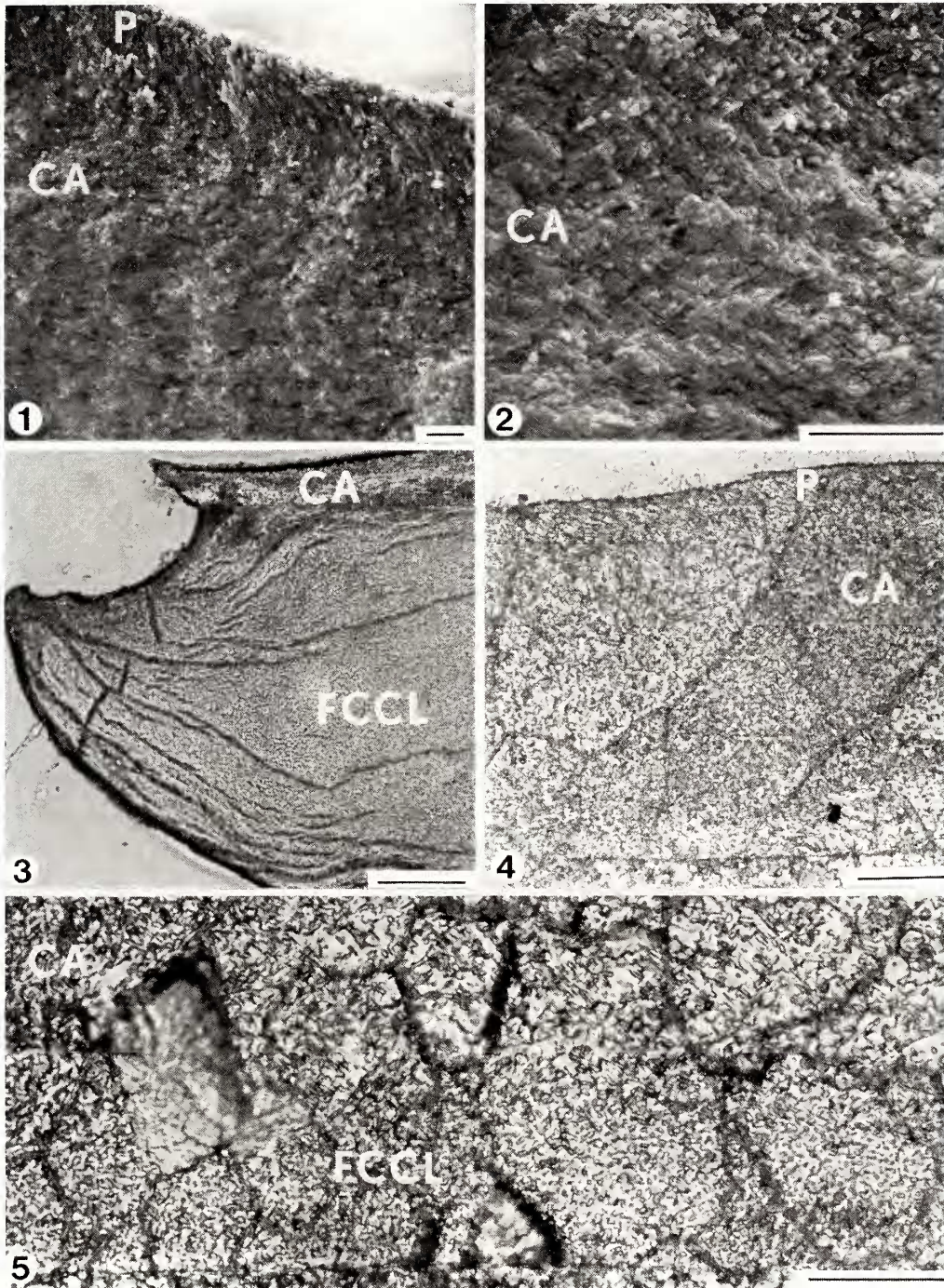
Fig. 2. Shell microstructure of Recent and Silurian malletiids. 2.1-2.3, reclined, prismatic (P), crossed acicular (CA), and fine complex crossed lamellar (FCCL) structures in Recent *Malletia obtusa* Sars, 1872, U.S. Fish Commission Station 2221, Atlantic Ocean. 2.1, SEM of radial fracture through posterior shell margin, shell exterior is up and posterior margin is toward the right; bar scale = 10 µm. 2.2, SEM of commarginal, vertical fracture near ventral shell margin, showing the two predominant dip directions of the crossed acicular, middle shell layer; shell exterior is up, bar scale = 5 µm. 2.3, dorsoventral, vertical acetate peel through the posterior hinge; dorsal exterior of shell is up and hinge dentition is toward the left; the prismatic outer shell layer is not recognizable in this section, bar scale = 50 µm. 2.4, 2.5, relict prismatic (P), crossed acicular (CA) and fine complex crossed lamellar (FCCL) structures in the Upper Silurian malletiid *Ekstadia tricarinata* Soot-Ryen, 1964, RMMo 15469. 2.4, acetate peel of a radial, vertical section near the anteroventral shell margin, showing the prismatic outer and crossed acicular middle shell layers, the shell exterior is up and the anteroventral shell margin is toward the right, bar scale = 50 µm. 2.5, acetate peel of an anteroventral, commarginal (transverse) section showing the boundary between the crossed acicular middle shell layer and the underlying FCCL inner shell layer, note that the dip directions in the CA structure cross diagenetic calcite crystal boundaries; the shell interior is near the bottom of the photograph; bar scale = 50 µm.

the fossette, although the thickness of this sublayer is unknown. A thin lamellar sublayer is hypothesized in Figs. 3.3-3.6. There is no evidence for a resilium.

The shell margins are smooth and thinly tapering. The outer shell layer is relatively thin and inconspicuous, and consists of fine, reclined prisms (Figs. 2.4, 4.4). The middle and inner shell layers are predominantly crossed acicular and fine complex crossed lamellar, respectively (Figs. 2.4, 2.5; 4.1-4.4). They are locally separated by an irregular simple prismatic pallial myostracum (Fig. 4.3). An internal shell blister was observed in one specimen (Fig. 4.1-4.3). The hinge consists primarily of fine complex crossed lamellar and possibly also homogeneous structure.

Family Praenuculidae McAlester, 1969

McAlester (1969) described the Praenuculidae as having an external ligament and no resilifer, thereby correcting Cox's (1959) reference to a resilifer in *Praenucula* Pfab, 1934. McAlester's (1969) placement of praenuculids in the superfamily "Nuculacea" also implied a truncate shell posterior and no pallial sinus. Cope (1997) restricted the Praenuculidae to "gradidentate" taxa, *i.e.*, with hinge teeth gradually increasing in size anteriorly and posteriorly from the subumbonal region. This family includes *Praenucula* Pfab, 1934, *Ledopsis* Beushausen, 1884, *Palaeoconcha* Miller, 1889, *Similodonta* Soot-Ryen, 1964, *Homilodonta* Cope, 1997, *Concavodonta* Babin and Melou, 1972, *Fidera* Pojeta and Gilbert-Tomlinson, 1977, and *Arcodonta* Cope, 1999, among others. According to Waller (1998:17), praenuculids range from Early Ordovician to at least Devonian and possibly Late Permian.

The Praenuculidae are commonly regarded as plesiomorphic members of the superfamily Nuculoidea (McAlester 1969; Pojeta and Gilbert-Tomlinson, 1977; Babin and Gutiérrez-Marco, 1991; Cope, 1996a; Liljedahl, 1994; Waller, 1998). However, Waller (1998) could not identify a synapomorphy uniquely linking the Praenuculidae with the nuculoidean families Nuculidae and Pristiglomidae. Carter *et al.* (2000) indicated that *Praenucula* is basal to the clade that contains both the superfamily Nuculoidea and the order Solemyoida, with the latter including "ctenodontids." Carter *et al.* therefore removed the Praenuculidae from the superfamily Nuculoidea and the order Nuculoida.

Praenuculid shell microstructure has been reported only for *Palaeoconcha* sp. from the Upper Ordovician Maquoketa Formation near Graf, Iowa (Mutvei, 1983). The phosphatized shell contains relict nacre tablets that are much wider than modern nacre tablets. Because gastropod and cephalopod nacre tablets from the same locality are similarly wide, secondary enlargement during phosphatization seems likely.

Praenucula faba Liljedahl, 1994 (Figs. 1.3, 5)

The present observations of *Praenucula faba* are based on dorsoventral acetate peels through two specimens with united valves (RMMo 15908, 25661). All sections passed from the hinge to the ventral margins. Specimen RMMo 25661 shows evidence for a dorsal, slightly submarginal, opisthodetic, simple ligament with continuous mineralization (Fig. 5). The thickness of the lamellar sublayer of the posterior ligament remains unknown; a relatively thin sublayer is hypothesized in Figs. 5.3-5.5. There is also evidence for lamellar ligament within an anterior, submarginal fossette (Fig. 5.1, 5.7). There is no evidence for a resilium.

The ventral shell margins are smooth and thinly tapering. The outer shell layer is thin and slightly reclined to nearly vertical, finely prismatic. The middle and inner shell layers and the hinge are nacreous. There is no well developed pallial myostracum.

Order Nuculoida Gray, 1824
Superfamily Nuculoidea Gray, 1824

The superfamily Nuculoidea is presently restricted to the families Nuculidae Gray, 1824, and Pristiglomidae Sanders and Allen, 1973, *i. e.*, excluding the Praenuculidae MacAlester, 1969. Sanders and Allen (1973) and Allen and Hannah (1986) differentiated the Nuculidae and Pristiglomidae on the basis of ctenidium size and structure, shape of cerebral ganglion and hindgut, and triangular or ovate as opposed to rounded shell shape, respectively. Waller (1998:17) listed three synapomorphies for the clade of Nuculidae plus Pristiglomidae: (1) heel of the foot distinct and sharply separated from the sole, (2) multiple loops in the hindgut, and (3) resilium with non-calcified central portion and calcified lateral portions containing mainly granular rather than fibrous aragonite. This last feature must now be regarded as a derived condition within the superfamily Nuculoidea, because one of the earliest nuculoideans, *Nuculoidea pinguis* (Lindström, 1880), has a mainly fibrous lateral resilium. Medially unmineralized, laterally fibrous resilia are widespread in the Palaeotaxodonta, having evolved not only within the superfamily Nuculoidea but also in various members of the superfamily Nuculanoidea Adams and Adams, 1858 (Carter, 1990).

Family Nuculidae Gray, 1824

Maxwell (1988) divided the Nuculidae into the subfamily Nuculominae Maxwell, 1988, which lacks large, radial prisms, and the subfamily Nuculinae Gray, 1824, which has such prisms. These are denticular composite prisms as defined by Carter *et al.* (1990b), *i.e.*, second-order prisms organized into first-order prisms by virtue of reflection and denticulation of the shell margins. Maxwell's
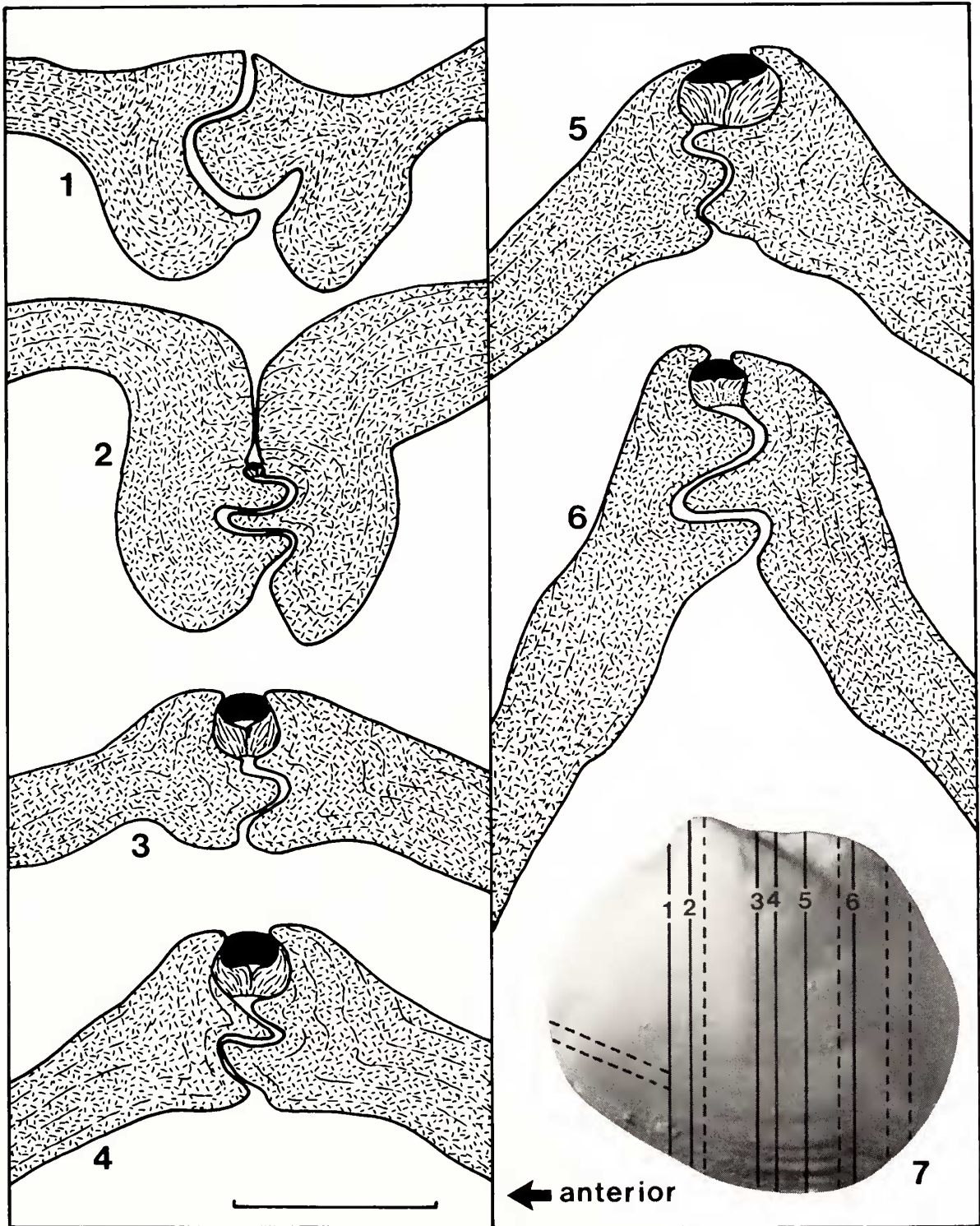
Fig. 3. Camera-lucida drawings of dorsoventral acetate peels through the hinge and ligament of *Ekstadia tricarinata* Soot-Ryen, 1964, Upper Silurian, Wenlockian, probably Mulde Formation, Gotland, Sweden, RMMo 15469 (3.1-3.6) and RMMo 15468 (3.7), both shells 8.2 mm in length. Fig. 3.7 shows the positions of illustrated sections through RMMo 15469 as numbered lines; the dashed lines represent sections that are not presently illustrated. In Figs. 3.1-3.6, irregularly oriented dashes between the growth lines represent fine CCL and/or homogeneous structure. A thin, impersistent, reclined prismatic outer shell layer is also present, but is not shown because it is too thin to be accurately represented. The dashes within the ligament fossettes (3.2-3.6) represent relict ligament fibers; the solid black areas above these dashes represent hypothesized lamellar ligament.
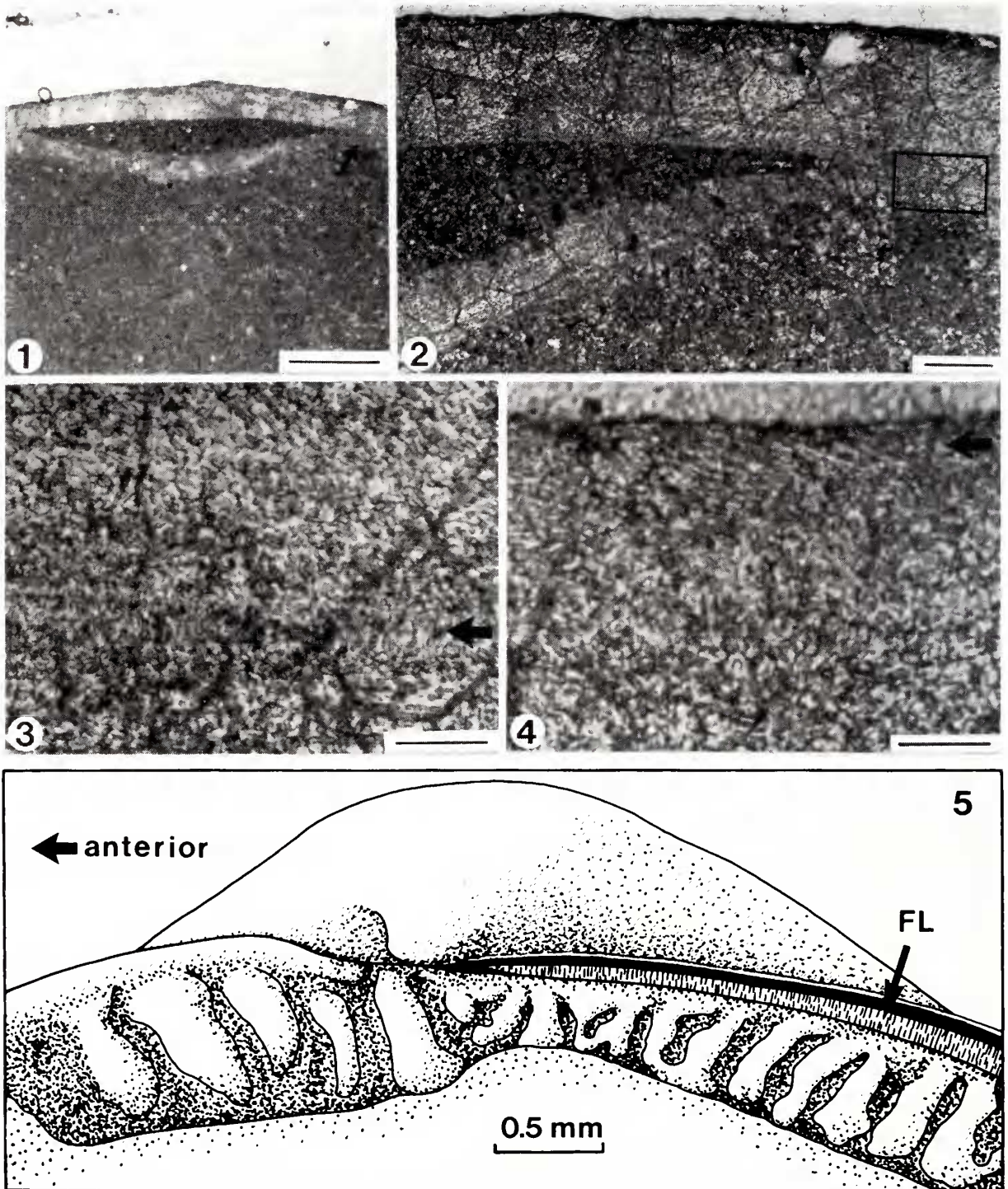
Fig. 4. *Ekstadia tricarinata* Soot-Ryen, 1964, Upper Silurian, Wenlockian, probably Mulde Formation, Gotland, Sweden, RMMo 15469. 4.1-4.3, progressively higher magnifications of an acetate peel of a dorsoventral section along the dashed line between sections 5 and 6 in Fig. 3.7, showing an interior shell blister (4.1); a thin, horizontal sublayer of irregular simple prisms (arrow in 4.3) underlain by poorly preserved crossed acicular structure (see Fig. 2.5 for a better view of the latter); Fig. 4.3 is an enlargement of the area indicated by the arrow in 4.1 and by the rectangle in 4.2; the shell exterior is up and the ventral shell margin is toward the right in all three figures; bar scales = 500 μm, 100 μm, and 25 μm, respectively. 4.4, acetate peel of a radial, vertical section near the anteroventral shell margin, showing the reclined prismatic (arrow) outer shell layer and the underlying crossed acicular (CA) middle shell layer; the shell exterior is up and the anteroventral shell margin is toward the right; bar scale = 25 μm. 4.5, reconstructed hinge and opisthodetic, submarginal, simple ligament, based on 10 dorsoventral sections through the hinge of RMMo 15469 (see Fig. 3.7 for positions of sections, using RMMo 15468) and fig. 34D of Liljedahl (1994); FL = fibrous ligament, overlain by reconstructed lamellar ligament (thick black line).

(1988) Silurian-Recent subfamily Nuculominae is presently restricted to largely nacreous nuculids without denticular composite prisms. Largely porcelaneous nuculids without denticular composite prisms are presently placed in the new Carboniferous-Recent subfamily Palaeonuculinae. The Palaeonuculinae replaced ancestral nacre with porcelaneous and matted structure in their adult stage, whereas the Carboniferous(?) or Cretaceous-Recent subfamily Nuculinae remained largely nacreous internally, and evolved denticular composite prisms. The denticular composite prisms thickened and interlocked the ventral shell margins, thereby enhancing protection against predation. The coarse, marginal denticulations in the Nuculinae differ from the marginal micropectinations present in some, but not all, Nuculominae, e.g., in Devonian *Nuculoidea opina* (Hall, 1843). These micropectinations affect primarily the nacreous, inner margin of the shell, rather than the prismatic outer shell layer (Schenck, 1934; Carter, 1990:145).

Subfamily Nuculominae Maxwell, 1988

This subfamily includes *Nuculoidea* Williams and Breger, 1916, *Nuculoma* Cossmann, 1907, *Nuculopsis* Girty, 1911, *Economolopsis* Hoare, Heaney, and Mapes, 1989, *Leionucula* Quenstedt, 1930, *Ennucula* Iredale, 1931, and *Brevinucula* Thiele, 1935, among others. Keen (1969) indicated that the genus *Nuculoidea* ranges from Ordovician to Devonian, but Pojeta and Runnegar (1985) noted that resilia are unknown in Ordovician palaeotaxodonts. The earliest presently known member of the Nuculominae, and hence of the Nuculidae and the superfamily Nuculoidea, is Silurian *Nuculoidea*.

Carter (1990, p. 147) found no evidence for mineralization in the simple ligament and resilium of two Devonian species of *Nuculoidea*. Lack of resilial mineralization in Devonian *Nuculoidea* now seems unlikely, given the present observations of Silurian *Nuculoidea*. Middle Devonian *Nuculoidea* has an adult outer shell layer of vertical simple(?) prisms, reclined fibrous prisms, and irregular simple prisms, and a juvenile outer shell layer of nearly vertical to reclined, irregular simple prisms. The middle and inner shell layers are nacreous except for minor porcelaneous structure near the ligament insertion area of one species.

Nuculoidea pinguis (Lindström, 1880) (Fig. 6)

Soot-Ryen (1964) and Liljedahl (1994:34) noted a small, slightly to moderately excavated resilifer and no external ligament in *Nuculoidea pinguis*. The present observations are based on dorsoventral acetate peels through three specimens with united valves. This includes 15 sections through RMMo 21914 (Figs. 6.2-6.6), 9 sections through RMMo 21913 (Fig. 6.1), and 4 sections through RMMo 15520. A symmetrical, internal resilium is present,

as well as an anterior, dorsal, submarginal, lamellar ligament. Mineralization in the resilium is lateral and mainly fibrous, with granular mineralization only near the medial, unmineralized part of the ligament. The latter is not shown in Fig. 6.3 in order to illustrate the spatial distribution of the adjacent lateral mineralization. The presence of a dorsal, submarginal, anterior lamellar ligament is indicated by minute fossettes with concentrated, framboidal pyrite (Fig. 6.2). These fossettes do not extend posterior to the beaks.

The shell margins are smooth and thinly tapering. The outer shell layer is relatively thin, and consists of finely textured, nearly vertical to slightly reclined prisms. The middle and inner shell layers are predominantly nacreous. A well developed pallial myostracum is not apparent.

Subfamily Nuculinae Gray, 1824
Nucula proxima Say, 1822 (Fig. 7)

The subfamily Nuculinae includes *Nucula* Lamarck, 1799, *Gibbonucula* Eames, 1951, *Lamellinucula* Schenck, 1944, *Linucula* Marwick, 1931, *Pectinucula* Quenstedt, 1930, *Pronucula* Hedley, 1902, and *Acila* Adams and Adams, 1858, among others. Nuculine shell and ligament microstructure has been studied by Schmidt (1922), Bøggild (1930), Wrigley (1946), Lucas (1952), Trueman (1952), Van de Poel (1955), Taylor et al. (1969), Speden (1970), Wise (1970), Kobayashi (1971), Flajs (1972), Suzuki (1983), Waller (1990), and Carter (1990). As illustrated by Recent *Nucula proxima*, the outer shell layer in this subfamily is denticular composite prismatic, and the middle and inner shell layers are nacreous except for prismatic myostracal deposits (Fig. 7). Porcelaneous structure is absent except in a small area of fine CCL or homogeneous structure immediately below the umbones in the inner shell layer (Carter et al., 1990a:306). Pallial myostracal prisms are only locally present.

Subfamily Palaeonuculinae nov.

The subfamily Palaeonuculinae is presently named for the Group of *Palaeonucula* Quenstedt and *Condylonucula* Moore, as defined by Carter (1990:148). *Palaeonucula* Quenstedt, 1930, is designated as the type genus. Palaeonuculines differ from other nuculids in having a largely non-nacreous adult shell. The juvenile shell may be nacreous or non-nacreous. Like the Nuculominae, they lack denticular composite prisms. Palaeonuculines resemble pristiglomids in having a non-nacreous adult shell, but pristiglomids lack nacre in their juvenile stage and matted structure in their adult stage.

Bøggild (1930:276) mentioned that Middle Jurassic "*Nucula hammeri*" (presumably of DeFrance, 1825, although not so indicated by Bøggild), the type species of *Palaeonucula* Quenstedt, 1930, has a homogeneous or very indistinctly prismatic shell. Lucas
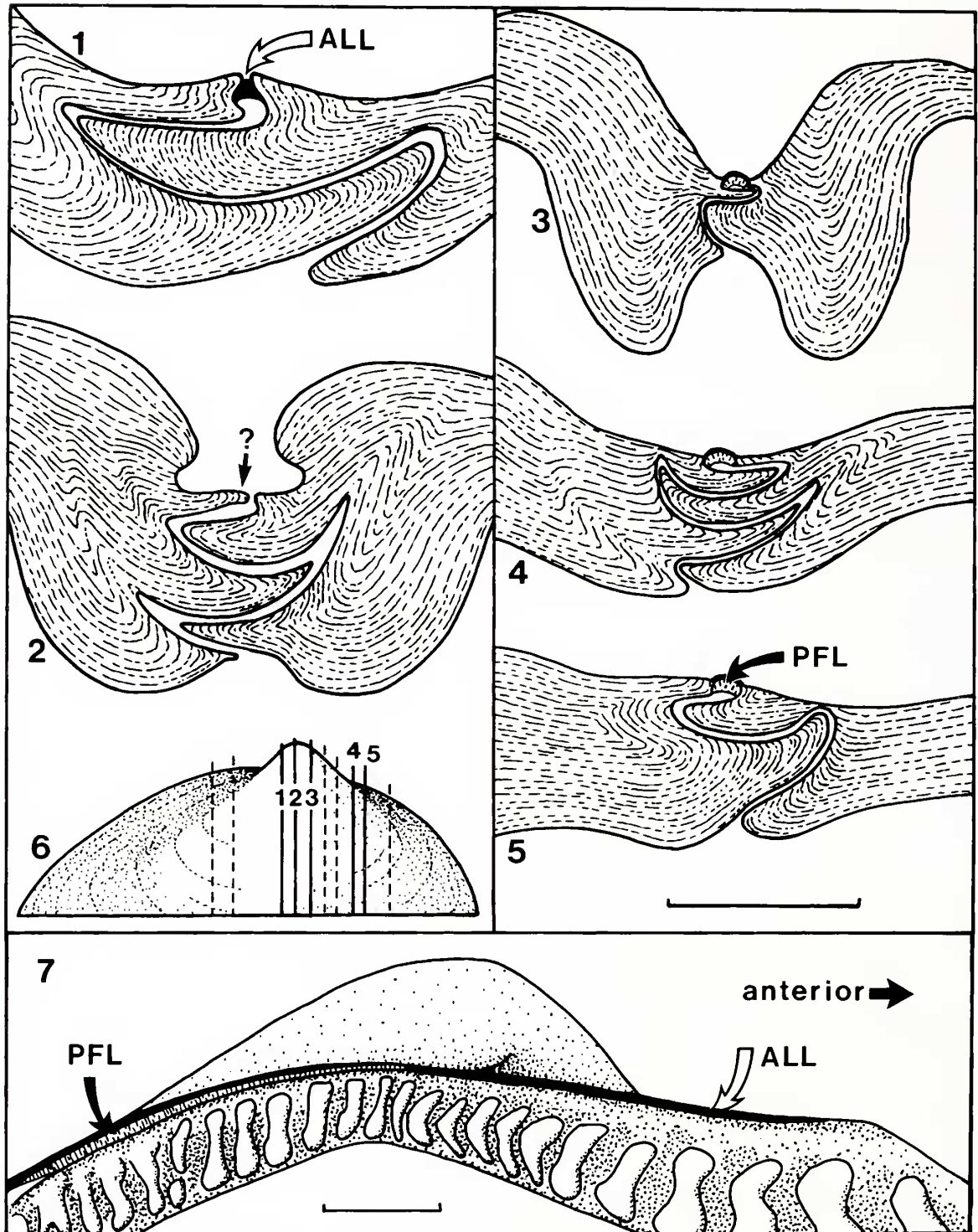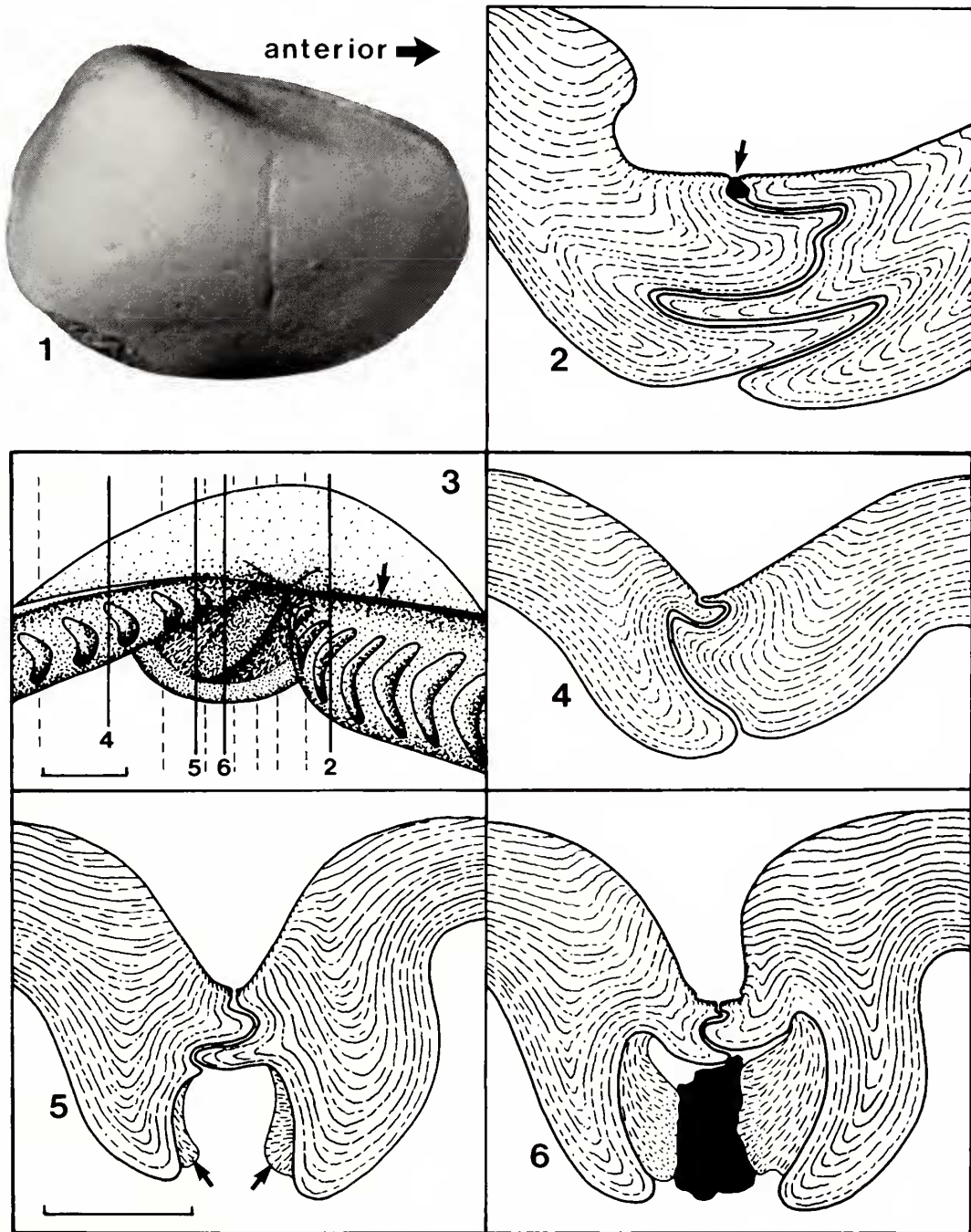
Fig. 5. Reconstructed shell and ligament microstructure of *Praenucula faba* Liljedahl, 1994, Upper Silurian, Wenlockian, Mulde Formation, Gotland, Sweden, based on camera lucida drawings of 10 dorsoventral sections through RMMo 25661 (section positions indicated by numbered lines on the left valve in Fig. 5.6; the dashed vertical lines in Fig. 5.6 indicate sections not presently illustrated; sectioned shell was 8.25 mm in length; ALL = anterior lamellar ligament, based on concentrations of framboidal pyrite; PFL = posterior fibrous ligament based on relict ligament fibers. The thickness of the lamellar sublayer of the posterior ligament, shown in Figs. 5.3-5.6 as a thick, black line, is hypothetical. The broken curving lines in 5.1-5.5 represent relict nacreous laminae. All vertical sections passed from the hinge to the ventral shell margins. The bar scale below Fig. 5.5 represents 0.5 mm and applies to sections 5.1-5.5. The bar scale for Fig. 5.7 represents 0.5 mm. The prismatic outer shell layer is too thin to be shown in these sections.

Fig. 6. Shell and ligament microstructure of *Nuculoidea pinguis* (Lindström, 1880), Upper Silurian, Wenlockian, Gotland, Sweden. 6.1, exterior of right valve, 8.2 mm in length, RMMo 21913, probably Mulde Formation; the anterior is toward the right. 6.2, 6.4-6.6, camera lucida drawings of dorsoventral sections through a shell 9.0 mm long (RMMo 21914, Mulde Formation), with section positions indicated by number in Fig. 6.3; dashed vertical lines in 6.3 show sections not presently illustrated. 6.2, dorsoventral section immediately anterior to beaks, showing submarginal, lamellar ligament (solid black, at arrow) inferred from concentrations of framboidal pyrite; the left and right valves appear asymmetrical because the section is oblique to the commissure plane. 6.4, dorsoventral section slightly posterior to the resilifer. 6.5, dorsoventral section through posterior part of resilifer, showing fibrous part of resilium (arrows). 6.6, dorsoventral section through central part of resilium, showing left and right fibrous and granular resilium separated by lamellar resilium (the latter shown by solid black area, shape and position based on concentrations of framboidal pyrite). 6.3, reconstructed hinge and ligament of a left valve; bar scale = 0.5 mm; fibrous resilium covers the surface of the resilifer, and grades from fibrous (dashes) to granular (stippled). In Fig. 6.3, the fossette for the anterior, dorsal, submarginal, lamellar ligament is shown by a thick black line (at arrow). The longer dashed lines in Figs. 6.2 and 6.4-6.6 are tracings of nacreous laminae; the shorter dashed lines near the dorsal surface of the hinge indicate the thin, finely prismatic outer shell layer. The bar scale in 6.5 represents 0.5 mm, and also applies to Figs. 6.2, 6.4, and 6.6.
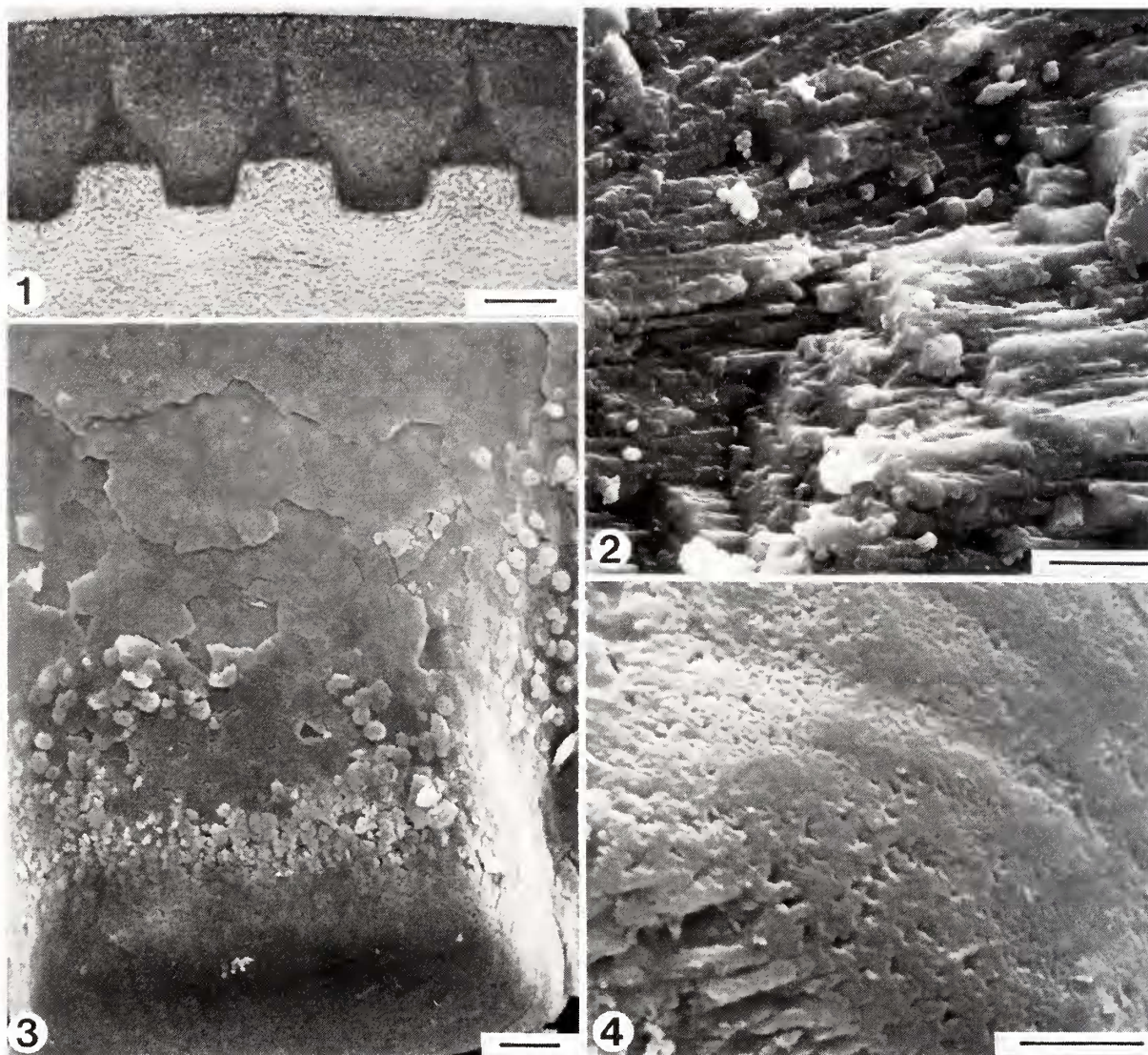
Fig. 7. Denticular composite prismatic outer layer and nacreous middle layer of Recent *Nucula proxima* Say, 1822, Long Island Sound, New York, YPM 10014. 7.1, acetate peel of a transverse, vertical section near the ventral shell margin, showing four radial, denticular composite prisms (above) and nacreous laminae (below); bar scale = 50 μm. 7.2-7.4, SEM of a radial, vertical fracture (7.2) and depositional surface (7.3, 7.4) of a single, denticular composite prism; bar scales = 5 μm in 7.2 and 7.3; bar scale = 10 μm in 7.4. In Fig. 7.3, the depositional surface of the prismatic outer layer is near the bottom of the photograph, and that of the nacreous middle layer is in the middle and upper part of the photograph; note the decrease in size of the nacre tablets toward the shell margin. Fig. 7.4 shows the depositional surface of a single denticular composite prism.

(1952) indicated that Upper Triassic *Palaeonucula strigilata* (Goldfuss, 1838) has an outer shell layer of reclined, radial fibrous prisms, a middle homogeneous layer, and an inner nacreous layer. Carter *et al.* (1990:309) examined this same species and found an outer shell layer with two sublayers: outer irregular simple prismatic to homogeneous, and inner finely irregular simple prismatic to fibrous prismatic. The middle and inner shell layers are homogeneous, but with a locally nearly matted structure that might be mistaken for nacre. Two other Triassic species of *Palaeonucula* were found by Carter *et al.* (1990a) to have largely porcela-

neous shells, with an outer shell layer that varies from nearly vertical to reclined irregular simple prismatic to fibrous prismatic, to homogeneous. Upper Carboniferous *Palaeonucula* sp. cf. *P. wewokana* (Girty, 1911) has a homogeneous shell and a partially fibrous resilium. Upper Carboniferous *Palaeonucula?* cf. "*Nucula*" *subrotundata* (Girty, mss. in Morningstar, 1922) has an outer shell layer of nearly vertical, fibrous prisms locally grading into dissected crossed prisms. The rest of the shell consists primarily of homogeneous structure, but this is locally transitional to crossed acicular or fine CCL, with bands of

irregular simple prisms and rare irregular CCL near the umbones (Carter, 1990).

Condylonucula maya Moore, 1977 (Fig. 8.1, 8.2)

Moore (1977) indicated that Recent *Condylonucula* lacks nacre. *Condylonucula maya* is only about 0.5 mm long at maturity, making it one of the smallest bivalves. The juvenile stage has an outer layer of slightly reclined, fibrous to irregular simple prisms, and middle and inner nacreous layers (Fig. 8.2). Later in ontogeny, the juvenile nacre is covered by irregular simple prisms (lower part of Fig. 8.2), and the middle shell layer becomes homogeneous to matted (Fig. 8.1). The matted structure is organizationally transitional between nacreous and porcelaneous, *i.e.*, retaining the laminar first-order arrangment of nacre, but having more or less homogeneous rather than tablet-like basic structural units.

Family Pristiglomidae Sanders and Allen, 1973

Allen and Hannah (1986) provided the following diagnosis for the Pristiglomidae: shell round; gills small, with markedly reduced number of short filaments; hind gut looped or coiled about both sides of the stomach. Waller (1990) noted that the pristiglomid resilium has granular lateral mineralization. Pristiglomids have not otherwise been described microstructurally.

Pristigloma nitens (Jeffreys, 1876) (Fig. 8.3)

Recent *Pristigloma nitens* has a thin, outer shell layer of radially reclined, fibrous to irregular simple prisms; a crossed acicular middle shell layer; and an inner shell layer that varies from fine CCL to irregular CCL to homogeneous (Fig. 8.3). The hinge is mostly fine CCL, but shows some crossed acicular and irregular CCL structure where it grades laterally into the umbonal part of the inner layer. Laminar microstructures, including nacre and matted structure, are absent at all ontogenetic stages.

Order Solemyoida Gray, 1840

McAlester (1969) placed the family Ctenodontidae Wöhrmann, 1893 in the order Nuculoida, and Newell (1969) placed the superfamily Solemyoidea in the order Solemyoida, subclass Cryptodonta Neumayr, 1884. Allen (1978, 1985) indicated that similarities in the form of the foot, gills, and digestive diverticula suggest a common origin for nuculoids and solemyoids. Scarlato and Starobogatov (1979) included the Nuculoida and Solemyoida in the superorder Protobranchia Pelseneer, 1889, and they assigned both the Ctenodontidae and Praenuculidae to the superfamily Ctenodontoidea. Pojeta (1988) tentatively placed *Ctenodonta* Salter, 1852, and its allies in the nuculanoidean family Malletiidae, and he regarded *Ctenodonta* as ancestral to the order Solemyoida,

which he placed in the Palaeotaxodonta. Liljedahl (1994) similarly placed *Tancrediopsis*, a close relative of *Ctenodonta*, in the Malletiidae. Waller (1990) defined the order Solemyoida on the basis of various anatomical features and loss of nacre, and he indicated that the Ctenodontidae and Solemyidae have similar ligament nymphs. Waller (1998) later separated the Nuculanoidea from the clade of Nuculoidea plus Solemyoidea, and he placed the family Ctenodontidae within the superfamily Solemyoidea. Waller (1998) listed several synapomorphies for the Solemyoidea, including sulfur-oxidizing bacterial symbiosis, posterior adductor muscle smaller than the anterior adductor muscle, and several soft anatomical features. Cope (1996b, 1997) transferred the Solemyoida to the subclass Lipodonta Iredale, 1939, although he maintained a palaeotaxodont origin for the group.

The phylogenetic analysis of Paleozoic bivalves by Carter *et al.* (2000) resolved the orders Nuculoida *s.s.* and Solemyoida as sister groups, and, within the Solemyoida, resolved *Tancrediopsis* basal to the clade of *Ctenodonta* plus *Acharax*. Synapomorphies identified for the Solemyoida, inclusive of the "ctenodontids" *Tancrediopsis* and *Ctenodonta*, include: triangular posteroventral shell margin; greatly elongated shell anterior with nearly parallel dorsal and ventral margins; opisthogyrate beaks; concavo-convex anterior palaeotaxodont dentition; and a wide, external, parivincular ligament. This list of synapomorphies will undoubtedly be modified as additional solemyoids, such as *Psiloconcha* Ulrich, 1894, *Dystactella* Hall and Whitfield, 1872, and *Clinopistha* Meek and Worthen, 1870, are added to the analysis.

The order Solemyoida is presently defined to include anteriorly or anteroventrally elongated, parivincular palaeotaxodonts such as *Tancrediopsis, Ctenodonta*, and *Acharax* and their solemyid, nucinellid, and manzanellid descendants. Relatively derived solemyoids may retain a parivincular ligament (*e.g.*, solemyids), or they may replace it with a simple ligament (*e.g.*, nucinellids), thereby reverting to the plesiomorphic condition for the Palaeotaxodonta.

Solemyoidean shell microstructure has been studied by Bøggild (1930), Beedham and Owen (1965), Taylor *et al.* (1969), Speden (1970), Kobayashi (1971), and Carter (1990). At least some Paleozoic solemyoideans were largely nacreous, whereas modern solemyoideans are porcelaneous-prismatic. Kobayashi (1971) reported nacre in an Oligocene *Solemya (Petrasma) velum* Say, 1822. Shell and ligament microstructure has not previously been described for "ctenodontids" such as *Tancrediopsis*.

Tancrediopsis gotlandica (Soot-Ryen, 1964) (Fig. 9)

According to Liljedahl (1994), *Tancrediopsis gotlandica* should be regarded as the type species of both *Tancrediopsis* Beushausen, 1895, and *Gotodonta*
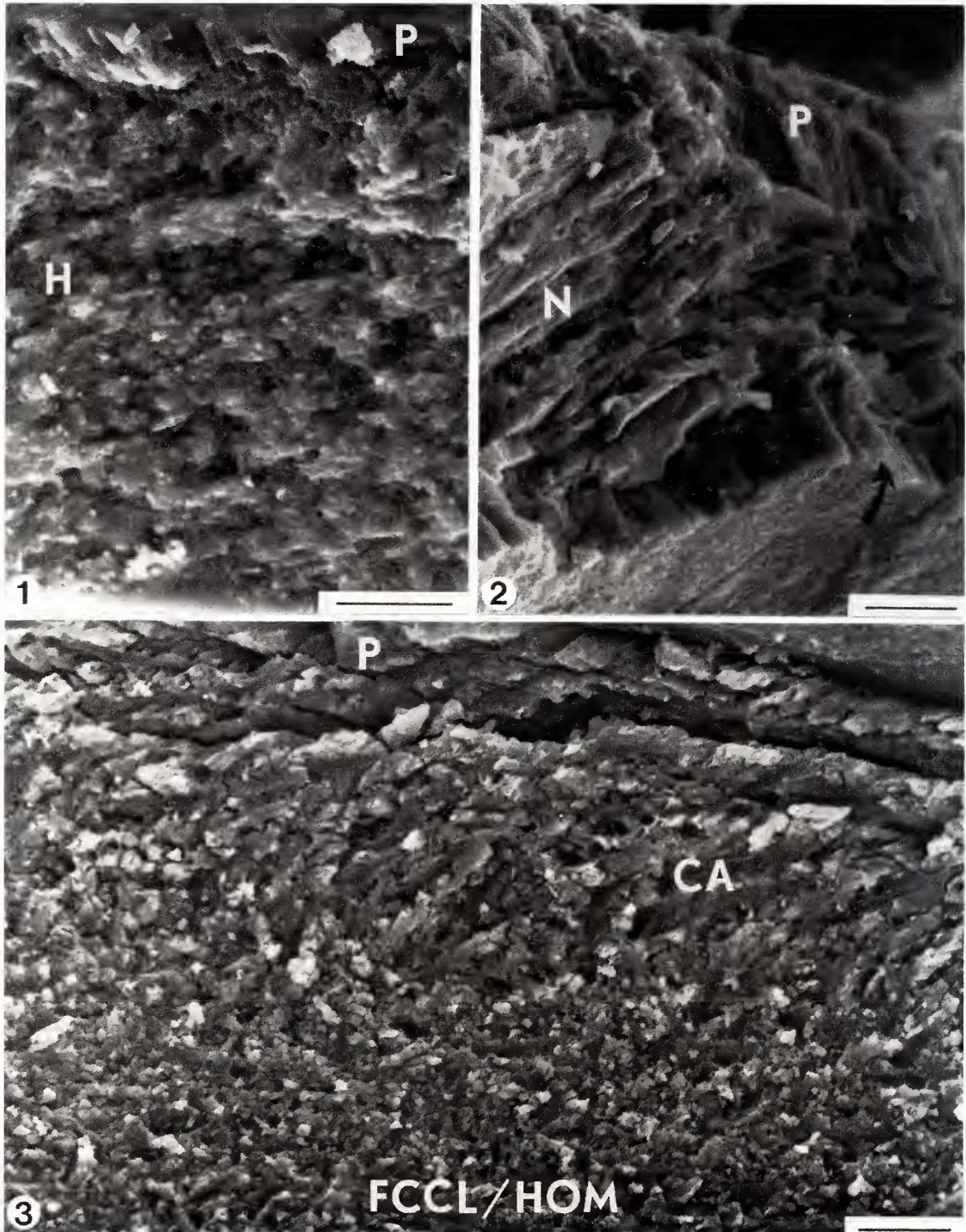
Fig. 8. Shell microstructure of predominantly porcelaneous nuculoideans. 8.1, 8.2, *Condylonucula maya* Moore 1977, collected by Dr. Donald Moore at the type locality, Chancanab Lagoon, 2 meters depth, Cozumel, Mexico (UNC 15236); SEM of dorsoventral, radial fractures; the shell exterior is up and the ventral margin is toward the right. 8.1, reclined prismatic outer shell layer (P) underlain by homogeneous to matted structure (H) near the adult ventral shell margin. 8.2, umbonal part of shell, showing reclined prismatic outer shell layer (P) and nacreous middle and inner layer of juvenile shell (N), the latter covered interiorly by a later ontogenetic irregular simple prismatic inner shell layer (at arrow); the inner depositional surface appears near the bottom of the photograph. 8.3, *Pristigloma nitens* (Jeffreys 1876), 2644 meters depth, Atlantic Ocean, 8° 28.8'N, 56°⁻ 4.5'W; SEM of ventral, radial, section, acid-etched and then treated with sodium hypochlorite to remove the organic matrix; shell exterior is up and ventral shell margin is toward the left; epoxy embedding block appears at far upper right; radially reclined prismatic outer shell layer (P) and crossed acicular (CA) middle shell layer, grading inward into fine CCL to homogeneous, inner shell layer (FCCL/HOM). Bar scales = 5 µm.

Soot-Ryen, 1964. Liljedahl (1994) indicated that *Gotodonta* and *Tancrediopsis* are based on the same species because the first designation of the type species of *Tancrediopsis* (by Cossmann, 1897) is invalid, as it does not agree with the original generic diagnosis. The type species of *Tancrediopsis* should instead be *Nucula sulcata* Hisinger, 1841, a junior homonym of *N. sulcata* Bronn, 1832. *N. sulcata* Hisinger was renamed by Soot-Ryen (1964) *Gotodonta gotlandica*, the type species of *Gotodonta*. McAlester (1969:N228) and Liljedahl (1994) regarded *Gotodonta* and *Praectenodonta* Philip, 1962, as synonyms.

Tancrediopsis gotlandica has an external, opisthodetic, parivincular ligament with a thick, strongly dorsally arched fibrous sublayer elevated by distinct nymphs (Fig. 9.2, 9.3, 9.6). The ligament fibers are oriented horizontally near the exterior of the ligament, but vertically near its inner part (Fig. 9.3, 9.6). The nymph is nacreous except for a thin, finely prismatic ligostracum where the fibrous ligament attached. The fibrous ligament did not extend anterior to the beaks, but the presence of anterior, submarginal fossettes suggests an anterior lamellar ligament (Fig. 9.5, 9.6). The fossettes are slightly asymmetrical, with the right fossette slightly higher and flatter than the left (Fig. 9.5). It remains uncertain whether the anterior fossettes contained lamellar ligament, because their framboidal pyrite is only slightly more concentrated than between the adjacent hinge teeth (Fig. 9.5).

The ventral and posterior shell margins are smooth and thinly tapering. The shell is moderately thick, with closely approximated shell margins all around. The outer shell layer is microstructurally distinct from the underlying nacre, but its microstructure appears largely featureless in acetate peels, with faint indications of irregular simple prisms and reclined fibrous prisms (Fig. 9.4). Not present are relatively large, regular simple prisms such as occur in *Acharax (Nacrosolemya) trapezoides* (Meek, 1874) (Carter, 1990:175, fig. 18A) and modern solemyoideans (Beedham and Owen, 1965; Taylor *et al.*, 1969:71; Carter and Lutz, 1990, pl. 20).

The middle and inner shell layers of *Tancrediopsis gotlandica* are nacreous, without a well-differentiated pallial myostracum. *T. gotlandica* differs from *Acharax trapezoides* and Recent *Solemya* in lacking porcelaneous structure in its ligament supports and major shell layers, but it resembles *A. trapezoides* in having nacreous middle and inner shell layers.

DISCUSSION

Cambrian bivalved molluscs probably evolved from minute, laterally compressed monoplacophorans similar to *Anabarella* Vostokova, 1962, *Watsonella* Grabau, 1900 (= *Heraultipegma* Pojeta and Runnegar, 1976), and *Pseudomyona* Runnegar, 1983 (Runnegar and Pojeta, 1974; Morris, 1979; MacKinnon, 1982, 1985; Runnegar, 1996; Kouchinsky, 1999). However, it remains uncertain whether the Cambrian molluscan bivalve grade is monophyletic or diphyletic. The largely calcitic, Middle Cambrian *Tuarangia* MacKinnon, 1982, may have been derived from a largely calcitic, foliated monoplacophoran similar to *Pseudomyona*, whereas Early Cambrian *Pojetaia* Jell, 1980, and *Fordilla* Barrande, 1881, most likely evolved from aragonitic ancestors similar to *Watsonella*. *Tuarangia* is clearly bivalved in the sense that it has distinct ligament insertion areas, differentiated left and right beaks, and possibly also separate anterior and posterior adductor muscle scars (Hinz-Schallreuter, 1995). However, *Pseudomyona* is commonly cited as its closest relative on the basis of similarities in shell shape and foliated microstructure (MacKinnon, 1982, 1985; Runnegar, 1983, 1985; Runnegar and Bentley, 1983; Runnegar and Pojeta, 1992). The hypothesis of an ancestral relationship between *Watsonella* and "fordilloids" has recently been strengthened by the discovery that *Watsonella* had a divided larval shell (Dzik, 1994:267), as well as certain microstructures in common with Early Cambrian *Pojetaia* and *Fordilla* (see Kouchinsky, 1999). The phylogenetic analysis by Carter *et al.* (2000) placed *Pseudomyona* and *Tuarangia* between *Watsonella* and *Pojetaia*, with these four genera comprising a paraphyletic grade. Their cladogram did not resolve *Pseudomyona* and *Tuarangia* as monophyletic, thereby leaving open the possibility that their foliated microstructure is homoplasious.

Recent studies of *Anabarella* and *Watsonella* have provided important new insights into microstructural comparisons with *Pojetaia runnegari* Jell, 1980. Runnegar (1983) and Kouchinsky (1999) demonstrated from steinkern impressions that the prismatic outer shell layer of *Anabarella* and *Watsonella* consisted of thin, flattened, columnar prisms with variably developed interprismatic matrices. These interprismatic matrices were probably thick near the lateral and subapical shell margins, judging from non-preservation of this prismatic layer on these parts of the steinkern margins (Kouchinsky, 1999, fig. 5). Impressions of similar outer-layer prisms can be seen on steinkerns of the Middle Cambrian, laterally compressed monoplacophoran *Mellopegma georginensis* Runnegar and Jell, 1976 (Runnegar, 1983, fig. 4D), a possible descendant of *Anabarella* or *Watsonella*. Kouchinsky (1999) showed that juvenile shells and the apical and dorsal parts of the adult shells of *Anabarella* and *Watsonella* consisted entirely of this prismatic outer shell layer. The dorsal, median part of the shell in *Anabarella* and *Watsonella* was therefore transitional between a "pseudoligament" as defined by Carter *et al.* (2000), *i.e.*, morphologically specialized for dorsal flexing but not completely microstructurally
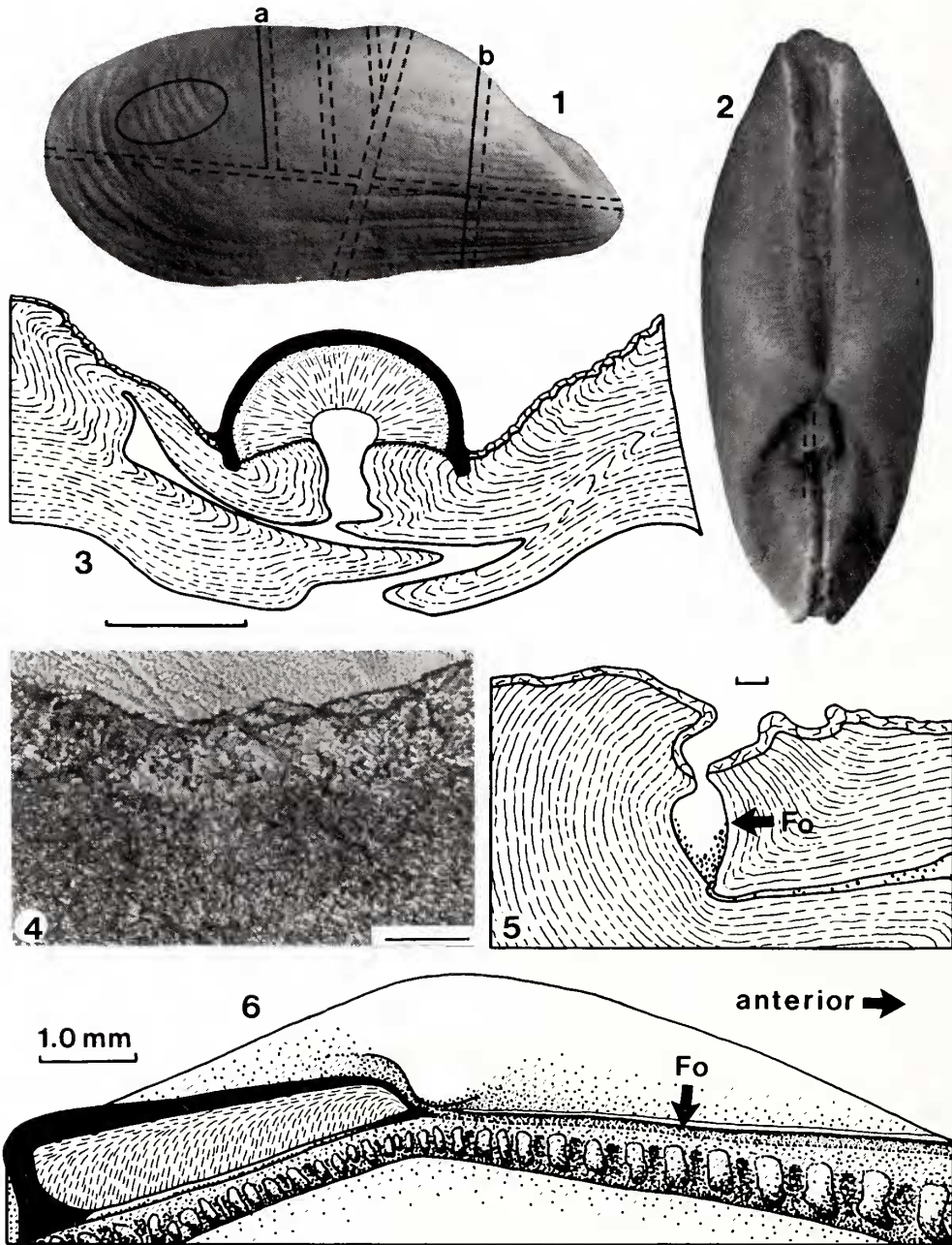
Fig. 9. Shell and ligament microstructure of the "ctenodontid" *Tancrediopsis gotlandica* (Soot-Ryen, 1964), Upper Silurian, Wenlockian, Mulde Formation, Gotland, Sweden, RMMo 15761 (Figs. 9.1-9.2) and RMMo 15768 (Figs. 9.3-9.5). 9.1, 9.2, left valve and dorsal view of united valves of a shell 25.2 mm in length; lettered lines indicate positions of illustrated sections for RMMo 15761 or 15768; dashed lines are sections not presently illustrated; specimen RMMo 15768 was also sectioned twice parallel to the commissural plane, through the hinge dentition (section positions not presently shown). 9.3, camera-lucida drawing of dorsoventral acetate peel through the parivincular ligament and hinge at section "b" in 9.1; the thickness of the lamellar outer sublayer of the ligament (thick black line) is guessed from concentrations of framboidal pyrite in the ligament grooves flanking the fibrous sublayer of the ligament; lines within the body of the shell represent nacreous laminae; a very thin, prismatic ligostracum separates the ligament from its nymph; the outer shell layer is represented by a thin, exterior band flanking the nymphs; bar scale = 1 mm. 9.4, acetate peel of a dorsoventral section near the posteroventral shell margin at section "b" in 9.1, showing the outer shell layer (above, with microstructure poorly preserved) and the underlying middle shell layer (showing very faint, relict nacreous laminae); the shell exterior is up and the posteroventral shell margin is toward the left; bar scale = 50 µm. 9.5, camera lucida drawing of dorsoventral section through the anterior hinge at section "a" in 9.1, showing the outer shell layer (upper band with irregular lines); the underlying nacreous hinge; and left and right fossettes (Fo) partially filled with framboidal pyrite (black spots); because framboidal pyrite also occurs between the hinge teeth, its presence does not, in this instance, necessarily indicate the former presence of unmineralized, lamellar ligament; bar scale = 100 µm. 9.6, medial hinge and opisthodetic, parivincular ligament, reconstructed from sections and from pl. 2, fig. 8 of Soot-Ryen (1964); Fo = fossette anterior to beaks, possibly (?) with lamellar ligament.

differentiated from the adjacent shell plates, and a true ligament, which is so differentiated.

Kouchinsky (1999) demonstrated that the "nacreous" structure that Runnegar (1983:126) reported for *Anabarella* is a combination of structures that Kouchinsky called "spiny" and "stepwise" textures. Similar microstructures occur in *Watsonella*. Kouchinsky (1999) referred these textures to the crossed microstructure category of Carter *et al.* (1990b). Indeed, the spiny texture locally shows a complex crossed lamellar arrangement (Kouchinsky, 1999, fig. 4E). However, the stepwise texture and other parts of the spiny texture are better regarded as laminar structures, *i.e.*, with first-order laminae oriented parallel or nearly parallel with the depositional surface (Carter *et al.*, 1990b). Some parts of the spiny texture in *Anabarella* resemble "*Sepia* sp. laminar structure" as defined by Carter *et al.* (1990b, fig. 14). The stepwise texture varies from lamello-fibrillar (= "type 2 nacre" of Mutvei, 1970) to large tablet, imbricated nacre. The latter structure is strikingly similar to the imbricated structure comprising the middle and inner shell layers of *Pojetaia runnegari* and *Fordilla troyensis* Barrande, 1881. These two "fordilloids" differ from *Anabarella* and *Watsonella* in depositing large tablet, imbricated nacre to the exclusion of complex crossed lamellar and lamello-fibrillar structures in their middle and inner shell layers. As illustrated by Runnegar and Bentley (1983, fig. 4G), the outer shell layer in *P. runnegari* consisted of flat, polygonal prisms with thick, interprismatic organic matrices, *i. e.*, similar to those comprising the outer shell layer of *Anabarella* and *Watsonella*. The fact that steinkern margins of *Pojetaia* show incipient imbricated nacre, and not prisms separated by thick organic matrices, probably reflects early post-mortem disintegration of the latter, as in *Anabarella* and *Watsonella*. The large tablet, imbricated structure in *Anabarella, Watsonella, Pojetaia,* and *Fordilla* should be classified as a form of nacre because of its laminar first-order organization, tablet-like structural subunits, and presumed aragonitic mineralogy. Large tablet, imbricated nacre is unknown among modern bivalves, but small-tablet, imbricated nacre is approximated in the early juvenile stage of *Condylonucula maya* (Fig. 8.2). The association of imbricated nacre with minute shells in Early Cambrian molluscs and Recent *Condylonucula* suggests that tablet imbrication reflects a biomechanical or depositional constraint related to small shell size. This imbricated stacking contrasts with the vertical stacking of columnar nacre, which associates with fast-growing surfaces, and with the horizontal to slightly imbricated stacking of sheet nacre, which associates with relatively slow-growing surfaces (Wise, 1970). The decrease in tablet size near the shell margins of *P. runnegari* and *F. troyensis* (see Runnegar and Pojeta, 1992, fig. 1) recalls the similar diminution in tablet

size near the ventral margins of *Nucula proxima* (Fig. 7.3).

Runnegar (1983, fig. 10F) illustrated relict columnar prisms in the opisthodetic ligament of *Pojetaia runnegari*. He suggested that these prisms are homologous with the prismatic structure that he believed comprised the shell plates, but with proportionally more organic matrix. Runnegar's (1983, fig. 10D,E) thin section through the calcite-replaced ligament shows no evidence for differentiated outer lamellar and inner, strongly mineralized sublayers. If the ligament in *Pojetaia* consisted of periostracum and a single, weakly mineralized, columnar prismatic layer, as Runnegar suggests, then the opisthodetic, simple ligament of early palaeotaxodonts may have evolved by adding a sub-periostracal, lamellar sublayer through modification of the dorsoposterior shell repair response, as suggested by Waller (1990, 1998), and by prolonging the period of growth in width of underlying ligament fibers to continue after the polymerization of their surrounding protein matrix, thereby increasing the opening moment and mineralization of the inner sublayer.

The flat, polygonal, exterior prisms in *Pojetaia runnegari* differ from the finer, radially reclined prisms in the outer shell layer of *Praenucula, Nuculoidea, Ekstadia,* and many other early or middle Paleozoic, wholly aragonitic bivalves. However, polygonal prisms co-occur with fine, radial prisms in the outer shell layer of the Devonian malletiid *Palaeoneilo filosa* (Conrad, 1842) (Carter, 1990, fig. 10B).

Interestingly, Middle Cambrian *Mellopegma georginensis* shows evidence for small-tablet sheet nacre similar to modern molluscs (Runnegar, 1983, fig. 4c). If Cambrian monoplacophorans transformed large tablet, imbricated nacre into modern nacre, then Cambrian "fordilloids" probably had a similar evolutionary potential. Cambrian "fordilloids" are in fact microstructurally varied. Geyer and Streng (1998) found that Middle Cambrian *Pojetaia sarhroensis* Geyer and Streng, 1998 differs microstructurally from Early Cambrian *P. runnegari*. Instead of flat, polygonal prisms in the outer shell layer, it has finely textured prisms, and instead of large tablet, imbricated nacre, it has "irregular prismatic" structures interiorly. The latter resemble crossed lamellar and irregular complex crossed lamellar structures in later porcelaneous bivalves (Geyer and Streng, 1998, fig. 4). However, these porcelaneous microstructures in *P. sarhroensis* are probably convergent on porcelaneous cardiolariids such as *Ekstadia* and porcelaneous malletiids such as *Palaeoneilo* Hall and Whitfield, 1869. The available evidence suggests that cardiolariids and malletiids evolved from nacreous palaeotaxodonts (Carter, 1990).

The hypothesis by Runnegar (1983, 1985) that *Pojetaia runnegari* and *Fordilla troyensis* had entirely prismatic shells is no longer tenable. Runnegar (1985, fig.

2C,D) illustrated a thin section through a recrystallized shell of *P. runnegari*, which reportedly shows prisms with uniformly parallel sides. Their shapes do not agree with his interpretation that the prisms increased in diameter from exterior to interior by geometric selection. The "prism" boundaries resemble calcite fracture planes locally developed in the homogeneous part of the outer shell layer in a Devonian *Palaeoneilo filosa* (Conrad, 1842) (Carter, 1990, fig. 10C). Columnar prisms in bivalve shells do not have imbricated depositional surfaces, whether these are slightly reclined, non-denticular composite prisms in trigonioids; radially elongate simple prisms in solemyids; aragonitic, regular simple prisms in pholadids; or calcitic simple prisms in pinnids (Carter and Lutz, 1990, pls. 20, 24, 29, 49). The closely spaced, transverse marks that Runnegar and Pojeta (1992:118) identified as casts of aragonite fibers in the "prisms" of *P. runnegari* and *F. troyensis* appear to be the structural subunits of large, imbricated nacre tablets. Similar structural units comprise the lamello-fibrillar structure in *Anabarella* (see Kouchinsky, 1999, fig. 2E), the imbricated nacre in *Watsonella* (see Kouchinsky, 1999, fig. 3H), and the sheet nacre in some Recent bivalves (Mutvei, 1983, fig. 3B).

The relationship of "fordilloids" to post-Cambrian bivalves remains problematic. Among the more recently published perspectives on this issue, Runnegar and Bentley (1983) suggested that *Pojetaia* gave rise to praenuculid palaeotaxodonts, whereas *Fordilla* gave rise to mytiloids, orthonotids and pholadomyoids. Pojeta (1985) presented a similar phylogeny in which *Pojetaia* and *Fordilla* gave rise to palaeotaxodonts and isofilibranchs, respectively. Cope (1996a) stated that *Pojetaia* is a palaeotaxodont, and he later (1997) included *Fordilla* in this group. Geyer and Streng (1998:87) placed *Pojetaia* and *Fordilla* in the Praenuculidae because these taxa resemble juveniles of later praenuculids. On the other hand, Waller (1990), Runnegar and Pojeta (1992), and Runnegar (1996) suggested that fordilloids comprise a sister group to crown group bivalves, although Runnegar and Pojeta (1992) kept open the possiblity that *Pojetaia* and *Fordilla* are the earliest palaeotaxodonts and isofilibranchs, respectively. Carter *et al.* (2000) noted that the "pretaxodont" hinge teeth in *Pojetaia* and *Fordilla* differ from palaeotaxodont *s.s.* hinge teeth. *Pojetaia* has at most four stout, broad based teeth in shells reaching 2.25 mm in length (Geyer and Streng, 1998, table 1), whereas post-Cambrian palaeotaxodonts commonly have at least six relatively sharply defined teeth in shells as small as 1.0 mm, with additional taxodont teeth in larger shells. Carter *et al.* (2000) suggested that *Pojetaia* and *Fordilla* are basal to crown group bivalves, and that these "fordilloids" represent a paraphyletic grade. According to their phylogenetic analysis, crown group bivalves are characterized by reduction in nacre tablet size as well as

changes in pedal and adductor musculature, continuity of the pallial line, and ligament mineralization. Because of the presence of large tablet, imbricated nacre in *Anabarella* and *Watsonella*, the retention of this distinctive microstructure in Early Cambrian *Pojetaia* and *Fordilla* should not be regarded as a synapomorphy for the Fordilloida, but a plesiomorphy for the Bivalvia.

The discovery of strong resilial mineralization in *Nuculoidea pinguis* was unexpected, because Carter (1990) found no evidence for resilial mineralization in two Devonian species of *Nuculoidea*. It now appears likely that the Devonian resilia were less well preserved, or that their lateral resilial mineralization had already evolved from mainly fibrous to mainly granular, with the latter being more difficult to identify as relics in diagenetic calcite. The ligament in *N. pinguis* resembles that in modern nuculoideans except for having mainly fibrous rather than mainly granular lateral mineralization. This is compatible with Waller's (1990:60) hypothesis that the nuculoidean resilium represents a submerged, opisthodetic simple ligament. However, resilia apparently evolved convergently in nuculoidean and nuculanoidean palaeotaxodonts (McAlester, 1964; Pojeta, 1978).

Praenuculids are microstructurally and ligamentally suitable ancestors for early nuculoids such as *Nuculoidea pinguis*. Because *Praenucula* was nacroprismatic and had an anterior, submarginal, lamellar ligament, submergence of its posterior, simple fibrous ligament would have produced a taxon similar to *Nuculoidea*. *Praenucula* may have also given rise to nacroprismatic "ctenodontids" such as *Tancrediopsis* by elevating its posterior ligament on nymphs. The parivincular ligament in *T. gotlandica* is strikingly similar to that in the Upper Carboniferous acharacid solemyoidean *Acharax (Nacrosolemya) trapezoides*. Both species have short, weakly projecting nymphs supporting a barrell-shaped, fibrous ligament with horizontally and vertically oriented fibers (Carter, 1990:172, fig. 17D; horizontal ligament fibers misidentified as "lamellar" ligament). *Tancrediopsis* differs from *Acharax* in having well developed, palaeotaxodont hinge teeth. However, Hoare *et al.* (1979, pl. 2, fig. 15) illustrated a specimen of *A. trapezoides* with a "chondrophore" consisting of a tooth-like, inverted V-shaped structure just ventral and posterior to the beaks, and Carter (1990:177) observed crenulations on the medial hinge of this species. Rather than a chrondrophore, these structures may represent vestiges of palaeotaxodont teeth. *T. gotlandica* differs from *A. trapezoides* and modern solemyids in having nacreous rather than predominantly porcelaneous nymphs. However, *Tancrediopsis, A. trapezoides*, and modern solemyids might be similar in having an anterior, asymmetrical, lamellar ligament. In *Solemya*, the anterior, lamellar ligament inserts onto a small yet distinct, longitudinal ridge just inside the dorsal anterior mar-

gin of the right valve, and onto the distal or inner edge of the dorsal anterior margin of the left valve (Carter, 1990:174). A similar longitudinal ridge occurs just inside the dorsal anterior margin of the right valve in *A. trapezoides*. The dorsal margin of the left valve of *A. trapezoides* lacks this ridge, but has an area of porcelaneous structure on the inner margin of this valve, just anterior to the beaks. This arrangement matches the porcelaneous structure in the longitudinal ridge on the margin of the right valve, as well as the porcelaneous structure in its parivincular nymph, suggesting an association with ligament attachment. The dorsal anterior shell margins of *A. trapezoides* are otherwise nacreous and prismatic. *T. gotlandica* has slightly asymmetrical, anterior fossettes but, as noted previously, it is not certain that these contained lamellar ligament.

Because solemyoideans share close common ancestry with "ctenodontid" palaeotaxodonts, the order Solemyoida should be retained in the subclass Palaeotaxodonta.

ACKNOWLEDGMENTS

LITERATURE CITED

Adams, H. and A. Adams. 1854-1858. *The Genera of Recent Mollusca Arranged According to their Organization.* London, J. van Voorst, 2, 1-661.

Allen, J. A. 1978. Evolution of deep-sea protobranch bivalves. *Philosophical Transactions of the Royal Society of London,* B, 284:387-401.

Allen, J. A. 1985. The Recent Bivalvia: their form and evolution. *In: The Mollusca, Volume 10, Evolution,* E. R. Trueman and M. R. Clarke, eds. pp. 337-403. Academic Press, New York.

Allen, J. A. and F. J. Hannah. 1986. A reclassification of the Recent genera of the subclass Protobranchia (Mollusca: Bivalvia). *Journal of Conchology, London* 32:225-249.

Babin, C. 1982. Mollusques bivalves et rostroconches. *In:* Brachiopodes (Articulés) et Mollusques (Bivalves, Rostroconches, Monoplacophores, Gastropodes) de l'Ordovicien Inférieur (Trémadocien-Arenigien) de la Montagne Noire (France Méridionale), C. Babin, R. Courtessole, M. Melou, J. Pillet, D. Vizcaino, and E. Yochelson. pp. 37-49, pls. 8-12. *Mémoire de la Société des Études Scientifiques de l'Aude.* Sival, Carcassonne, 1-63, pls. 1-15.

Babin, C. and M. Melou. 1972. Mollusques bivalves et brachiopodes des 'Schistes de Raguenez' (Ordovicien supérieur de Finistère); conséquences stratigraphiques et paléobiogéographiques. *Annales de la Société Géologique du Nord* 92:79-94.

Babin, C. and J. Gutiérrez-Marco. 1991. Middle Ordovician bivalves from Spain and their phyletic and palaeogeographic significance. *Palaeontology* 34:109-147.

Barrande. J. 1881. *Système Silurien du Centre de la Bohême. Vol. VI: Acéphalés.* Paris, Prague, 342 pp.

Beedham, G. E. and G. Owen. 1965. The mantle and shell of *Solemya parkinsoni* (Protobranchia: Bivalvia). *Proceedings of the Zoological Society of London* 144(3):405-430.

Beushausen, H. E. L. 1884. Beiträge zur Kenntniss des Oberharzer Spiriferensandsteins und seiner Fauna. *Geologische Spezialkarte, Preussen und den Thüringen Staaten, Abhandlungen* 6(1):1-133, 6 pls.

Beushausen, H. E. L. 1895. Die Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden. *Abhandlungen der Königlichen Preussischen Geologisches Landesanstalt, Neue Folge* 17:1-514, 38 pls in separate atlas.

Bøggild, O. B. 1930. The shell structure of the mollusks. *Det Kongelige Danske Videnskabernes Selskabs Skrifter. Naturvidenskabelig og Mathematisk Afdeling,* ser. 9, 2:231-326, 15 pls.

Bronn, H. G. 1832. *Ergebnisse Meiner Naturhistorisch-Ökonomischen Reisen. Pt. 2.* Heidelberg and Leipzig, 686 pp.

Carter, J. G. 1990. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia. *In: Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends, Volume 1,* J. G. Carter, ed. pp. 135-296. Van Nostrand Reinhold, New York.

Carter, J. G. and M. J. S. Tevesz. 1978a. Shell microstructure of a Middle Devonian (Hamilton Group) bivalve fauna from central New York. *Journal of Paleontology* 52:859-880.

Carter, J. G. and M. J. S. Tevesz. 1978b. The shell structure of *Ptychodesma* (Cyrtodontidae; Bivalvia) and its bearing on the evolution of the Pteriomorphia. *Philosophical Transactions of the Royal Society of London,* series B, 284:367-374.

Carter, J. G. and W. W. Ambrose. 1989. Techniques for studying Molluscan shell microstructure. *In: Paleotechniques,* R. M. Feldmann, R. E. Chapman, and J. T. Hannibal, eds. pp. 101-119. *The Paleontological Society Special Publication* No. 4.

Carter, J. G. and R. A. Lutz. 1990. Part 2, Bivalvia (Mollusca). *In: Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends, Volume II,* J. G. Carter, ed. pp. 5-28, pls. 1-121. Van Nostrand Reinhold, New York.

Carter, J. G., D. R. Lawrence, and H. Sanders. 1990a. Chapter 12, Shell microstructural data for the Bivalvia. Part II. Orders Nuculoida and Solemyoida, *In: Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends, Volume 1,* J. G. Carter, ed. pp. 303-319. Van Nostrand Reinhold, New York.

Carter, J. G., K. Bandel, v. de Buffrénil, S. J. Carlson, J. Castanet, M. A. Crenshaw, J. E. Dalingwater, H. Francillon-Vieillot, J. Géraudie, F. J. Meunier, H. Mutvei, A. de Ricqlès, J. Y. Sire, A. B. Smith, J. Wendt, A. Williams, and L. Zylberberg. 1990b. Glossary of skeletal biomineralization, *In: Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends, Volume 1,* J. G. Carter, ed. pp. 609-671. Van Nostrand Reinhold, New York.

Carter, J. G., D. C. Campbell, and M. R. Campbell. 2000. Cladistic perspectives on early bivalve evolution. *In: The Evolutionary Biology of the Bivalvia,* E. M. Harper, J. A. Crame, and J. D. Taylor, eds. Geological Society, London, Special Publications 177:47-79.

Conrad, T. A. 1842. Observations on the Silurian and Devonian Systems of the United States, with descriptions of new organic remains. *Journal of the Academy of Natural Sciences of Philadelphia* 8(2):228-280, pls. 12-17.

Cooper, G. A. 1931. Concerning the authorship of the "Preliminary notice

of the lamellibranch shells of the upper Helderberg, Hamilton, and Chemung Groups, etc., Part 2". *Journal of the Washington Academy of Sciences* 21:459-467.

Cope, J. C. W. 1996a. Early Ordovician (Arenig) bivalves from the Llangynog inlier, South Wales. *Palaeontology* 39(4):979-1025.

Cope, J. C. W. 1996b. The early evolution of the Bivalvia. *In: Origin and Evolutionary Radiation of the Mollusca*, J. Taylor, ed. pp. 361-370. Oxford University Press, The Malacological Society of London.

Cope, J. C. W. 1997. The early phylogeny of the class Bivalvia. *Palaeontology* 40(3):713-746.

Cope, J. C. W. 1999. Middle Ordovician bivalves from Mid-Wales and the Welsh Borderland. *Palaeontology* 42(3):467-499.

Cossmann, M. 1897. Catalogue illustré des coquilles fossiles des environs de Paris. *Societe Royale Belgique, Annales* 22(2):1-214.

Cossmann, M. 1907. Paléontologie. In: Note sur le Callovien de la Haute-Marne et Spécialement sur un Gisement situé dans la Commune de Bricon, P. Thiéry and M. Cossmann, *VI Congrès de l'Association Franc-Comtoise (Vesonl 1906) Societè d'Agriculture, Lettres, Sciences et Arts du Département de la Haute-Saône, Bulletin* 1907(2):69-147, pls. 1-3.

Cox, L. R. 1959. The geological history of the Protobranchia and the dual origin of taxodont Lamellibranchia. *Proceedings of the Malacological Society of London* 33(5):200-209.

Defrance, M. 1825. Nucule, *Nucula. Dictionnaire des Sciences Naturelles*, Paris, vol. 35, pp. 215-219.

Douvillé, H. 1913. Classification des lamellibranches. *Bulletin de la Société Géologique de France*, ser. 4, 12:419-467.

Dzik, J. 1994. Evolution of "small shelly fossils" assemblages. *Acta Palaeontologica Polonica* 39:247-313.

Eames, F. E. 1951. A contribution to the study of the Eocene in western Pakistan and western India. B. The description of the Lamellibranchia from standard sections in the Rakhi Nala and Zinda Pir areas of the western Punjab and in the Kohat District. *Philosophical Transactions of the Royal Society of London*, B, no. 627, 235:311-482.

Flajs, G. 1972. On the ultrastructure of the hinge of the Bivalvia, 1. *Biomineralization Research Reports* 6:49-65, 5 pls.

Fuchs, A. 1919. Beitrag zur Kenntnis der Devonfauna der Verse- und der Hobräcker Schichten des Sauerländischen Faciesgebietes. *Jahrbuch des Preussischen Geologischen Landesanstalt (1918)* 39:58-95, pls. 5-9.

Geyer, G. and Streng, M. 1998. Middle Cambrian pelecypods from the Anti-Atlas, Morocco. *Revista Española de Paleontología, num. extr. Homenaje al Prof. Gonzalo Vidal*, pp. 83-96.

Girty, G. H. 1911. On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *New York Academy of Science, Annals* 21:119-156, 1912 [fide McAlester, 1968, p. 61, 50 reprints distributed August, 1911]

Goldfuss, G. A. 1826-1844. *Petrefacta Germaniae tam ea, quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmiae Rhenonae Servantur quam alia Quaecunquae in Museis Hoenighusiano Muensteriano Aliisque Extant, Iconibus et Descriptionibus Illustrata. Part I* (1826-1833), x + 252 pp., pls. 1-71; *Part 2* (1834-1840) [1833-1841], iii + 312 pp., pls. 72-165; *Part 3* (1841-1844) [1841, 1844], iv + 128 pp., pls. 166-200. Arnz and Co., Düsseldorf.

Grabau, A. W. 1900. Palcontology of the Cambrian terranes of the Boston Basin. *Boston Society of Natural History Occasional Papers* 4(3):601-694, 8 pls.

Gray, J. E. 1824. A natural arrangement of Mollusca according to internal structure. *Repository* 15:229-239.

Gray, J. E. 1840. *Synopsis of the contents of the British Museum, 42nd Edition*. British Museum, London, 370 pp.

Hall, J. 1843. *Geology of New York, Part 4, Comprising the Survey of the Fourth Geological District. Natural History of New York*, Albany, 683 pp.

Hall, J. 1847. *Palaeontology of New York, Volume I. Containing Descriptions of the Organic Remains of the Lower Division of the New-York System (equivalent of the Lower Silurian Rocks of Europe)*. Albany, C. van Benthuysen, i-xxiii + 1-338, 87 pls.

Hall, J. and R. P. Whitfield. 1869. *Preliminary Notice of the Lamellibranchiata Shells of the Upper Helderberg, Hamilton, and Chemung Groups, with Others from the Waverly Sandstones, pt. 2*. Albany, New York, 80 p. [McAlester, 1968, p. 62, accepted the conclusions of Cooper (1931) regarding the authorship of this anonymous paper].

Hall, J. and R. P. Whitfield. 1872. *Descriptions of new species of fossils, from the vicinity of Louisville, Kentucky, and the falls of the Ohio; from the collection of Dr. James Knapp, of Louisville (continued)*. Preprint, published in June 1872, in advance of the Report of the New York State Museum; pages numbered 1-13.

Hedley, C. W. 1902. Mollusca. Part 1. Brachiopoda and Pelecypoda. (Scientific Results of the Trawling Expedition of H.M.C. 'Thetis'). *Memoirs of the Australian Museum, Sydney*, IV, I:290-291.

Hinz-Schallreuter, 1. 1995. Muscheln (Pelecypoda) aus dem Mittelkambrium von Bornholm. *Geschiebekunde Aktuel* 11:71-84.

Hisinger, W. 1841. *Förteckning Öfver en Geognostik och Petrefactologisk Samling från Sverige och Norrige*. Stockholm, 69 pp. (Reprinted 1842.)

Hoare, R. D., M. T. Sturgeon, and E. A. Kindt. 1979. *Pennsylvanian Marine Bivalvia and Rostroconchia of Ohio*. State of Ohio, Department of Natural Resources, Division of Geological Survey, Bulletin 67:1-77, 18 pls.

Hoare, R. D., M. J. Heaney 111, and R. H. Mapes. 1989. Bivalves (Mollusca) from the Imo Formation (Mississippian, Chesterian) of north-central Arkansas. *Journal of Paleontology* 63(5):582-603.

Iredale, T. 1931. Australian Molluscan Notes 1. *Records of the Australian Museum* 18:201-235.

Iredale, T. 1939. Great Barrier Reef Expedition 1928-1929. *Scientific Reports, British Museum (Natural History)*, 5 [Mollusca, Part 1]:209-425.

Jeffreys, J. G. 1876. New and peculiar Mollusca of the *Kellia, Lucina, Cyprina*, and *Corbula* families procured in the 'Valorous' Expedition. *Annals and Magazine of Natural History, ser. 4*, 18:424-436.

Jell, P. A. 1980. Earliest known pelecypod on earth - a new Early Cambrian genus from South Australia. *Alcheringa* 4:233-239.

Keen, A. M. 1969. Family Nuculidae Gray, 1824. *In: Treatise on Invertebrate Paleontology, Part N, Volume I, Mollusca 6, Bivalvia*, L. R. Cox, N. D. Newell, D. W. Boyd, C. C. Branson, R. Casey, A. Chavan, A. H. Coogan, C. Dechaseaux, C. A. Fleming, F. Haas, L. G. Hertlein, E. G. Kauffman, A. M. Keen, A. LaRocque, A. L. McAlester, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner, and J. Weir, eds. pp. N230-231. The Geological Society of America, Inc., and The University of Kansas Press, Lawrence.

Kershaw, S. 1993. The Silurian Geology of Gotland, Sweden. *Geology Today* 9(5):187-190.

Kobayashi, 1. 1971. Internal shell microstructure of Recent bivalvian molluscs. Science *Reports of Niigata University, Ser. E, Geology and Mineralogy*, No. 2:27-50, 10 pls.

Korobkov, I. A. 1954. Sprvochnik i Metodicheskoe Rukovodstvo po Tretichnym Mollyuskam Plastinchatozhabernye [Handbook on

and Systematic Guide to the Tertiary Mollusca, Lamellibranchiata]. *Gosud. Nauchno-tecnoï Issledov. Nefti. Gorno-toplivnoi lit-ry*, Leningradskoi Otdelenie, 444 pp., 96 pls. [In Russian].

Kouchinsky, A. V. 1999. Shell microstructures of the Early Cambrian *Anabarella* and *Watsonella* as new evidence on the origin of the Rostroconchia. *Lethaia* 32:173-180.

Lamarck, J. B. de. 1799. Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux, par le citoyen Lamarck. *Société d'Histoire Naturelle de Paris, Mémoire* 1:63-91.

Liljedahl, L. 1994. Silurian nuculoid and modiomorphid bivalves from Sweden. *Fossils and Strata* 33:1-89.

Lindström, G. 1880. *In: Fragmenta Silurica e Dono Caroli Henrici Wegelin*, N. P. Angelin and G. Lindström, Stockholm. 39 pp.

Lucas, G. 1952. Étude microscopique et pétrographique de la coquille des lamellibranches. *In: Traité de Paléontologie*, Vol. 2, Masson et Cie. pp. 246-260.

McAlester, A. L. 1964. Preliminary suggestions for a classification of nuculoid bivalves. *Journal of Paleontology* 38(2):397-400.

McAlester, A. L.. 1968. Type species of Paleozoic nuculoid bivalve genera. *The Geological Society of America, Inc., Memoir*, 105: i-ix + 143 p.

McAlester, A. L. 1969. Superfamily Ctenodontacea and Family Praenuculidae. *In: Treatise on Invertebrate Paleontology, Part N, Volume 1, Mollusca 6, Bivalvia*, L.R. Cox, N. D. Newell, D. W. Boyd, C. C. Branson, R. Casey, A. Chavan, A. H. Coogan, C. Dechaseaux, C. A. Fleming, F. Haas, L. G. Hertlein, E. G. Kauffman, A. M. Keen, A. LaRocque, A. L. McAlester, R. C. Moore, C. P. Nutall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner, and J. Weir, eds. pp. N227-N230. The Geological Society of America, Inc., and The University of Kansas Press, Lawrence.

MacKinnon, D. I. 1982. *Tuarangia paparua* n. gen. and n. sp., a late Middle Cambrian pelecypod from New Zealand. *Journal of Paleontology* 56:589-598.

MacKinnon, D. I. 1985. New Zealand late Middle Cambrian molluscs and the origin of Rostroconchia and Bivalvia. *Alcheringa* 9:65-81.

Marwick, J. 1931. The Tertiary Mollusca of the Gisbourne District. *New Zealand Geological Survey, Palaeontological Bulletin, Geological Survey Wellington*, no. 13:1-177, 18 pls.

Maxwell, P. A. 1988. Comments on "A reclassification of the Recent genera of the Subclass Protobranchia (Mollusca: Bivalvia)" by J. A. Allen and F. J. Hannah (1986). *Journal of Conchology* 33:85-96.

Meek, F. B. 1874. Notes on some of the fossils figured in the recently-issued fifth volume of the Illinois State Geological Report. *The American Journal of Science and Arts*, ser. 3, 7(107):580-584.

Meek, F. B. and A. H. Worthen. 1870. Descriptions of new species and genera of fossils from the Palaeozoic rocks of the western states. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1870:22-45.

Miller, S. A. 1889. *North American Geology and Paleontology for the Use of Amateurs, Students, and Scientists*. Cincinnati [Ohio], 718 p.

Moore, D. R. 1977. Small species of Nuculidae (Bivalvia) from the tropical Western Atlantic. *The Nautilus* 91(4):119-128.

Morningstar, H. 1922. Pottsville fauna of Ohio. *Geological Survey of Ohio, 4th Ser., Bulletin* 25:1-312, 16 pls.

Morris, N. J. 1979. On the origin of the Bivalvia. *In:* The Origin of Major Invertebrate Groups, M. R. House, ed. pp. 381-413. *Systematics Association Special Volume No. 12*, Academic Press, London and New York.

Munnecke, A., C. Samtleben, T. Servais and D. Vachard. 1999. SEM-observation of calcareous micro- and nannofossils *incertae sedis* from the Silurian of Gotland, Sweden: preliminary results. *Geobios* 32(2):307-314.

Mutvei, H. 1970. Ultrastructure of the mineral and organic components of molluscan nacreous layer. *Biomineralization Research Reports* 2:48-61.

Mutvei, H. 1983. Ultrastructural evolution of molluscan nacre. *In: Biomineralization and Biological Metal Accumulation*, P. Westbroek and E. W. de Jong, eds. pp. 267-271. D. Reidel Co., Boston, Massachusetts.

Neumayr, M. 1884. Zur Morphologie des Bivalvenschlosses. *Kaiserlich-Königlichen Akademie der Wissenschaften, Wien, Mathematische-Naturwissenschaftliche Klasse, Sitsungsberichte*, Abteilung 1, 88(1883):385-418, 2 pls.

Newell, N. D. 1969. Subclass Cryptodonta. *In: Treatise on Invertebrate Paleontology, Part N, Volume 1, Mollusca 6, Bivalvia*, L. R. Cox, N. D. Newell, D. W. Boyd, C. C. Branson, R. Casey, A. Chavan, A. H. Coogan, C. Dechaseaux, C. A. Fleming, F. Haas, L. G. Hertlein, E. G. Kauffman, A. M. Keen, A. LaRocque, A. L. McAlester, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner, and J. Weir, eds. pp. N241. The Geological Society of America, Inc., and The University of Kansas Press, Lawrence.

Pelseneer, P. 1889. Sur la classification phylogénétique des pélécypodes (communication préliminaire). *Bulletin Scientifique de la France et de la Belgique* 20:27-52.

Pfab, L. 1934. Revision der Taxodonta des Böhmischen Silurs. *Palaeontographica*, Abt. A, 80:195-253, pls. 2-4.

Philip, G. M. 1962. The palaeontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. *Royal Society of Victoria, Proceedings, University Series* 75:123-246, pls. 11-36.

Poel, L. Van de. 1955. Structure du test et classification des Nucules. *Institute Royal des Sciences Naturelles de Belgique, Bulletin* 31(3):1-11.

Pojeta, J., Jr. 1978. The origin and early taxonomic diversification of pelecypods. *Philosophical Transactions of the Royal Society of London, ser. B*, 284:225-246.

Pojeta, J., Jr. 1985. Early evolutionary history of diasome mollusks. *In: Mollusks, Notes for a Short Course*. T. W. Broadhead, ed. *University of Tennessee Department of Geological Sciences, Studies in Geology* 13, 102-130.

Pojeta, J., Jr. 1988. The origin and Paleozoic diversification of solemyoid pelecypods. *New Mexico Bureau of Mines and Mineral Resources Memoir* 44:201-271.

Pojeta, J., Jr. and B. Runnegar. 1976. The paleontology of rostroconch mollusks and the early history of the Phylum Mollusca. *U.S. Geological Survey Professional Paper* 968:i-iv, 1-88, + 54 pls.

Pojeta, J., Jr. and J. Gilbert-Tomlinson. 1977. Australian Ordovician pelecypod molluscs. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* 174:1-64, pls. 1-29.

Pojeta, J., Jr. and B. Runnegar. 1985. The early evolution of diasome molluscs. *In: The Mollusca, Volume 10, Evolution*. E. R. Trueman and M. R. Clarke, eds. pp. 295-336. Academic Press, Inc., Orlando.

Quenstedt, W. 1930. Die Anpassung an die grabende Lebensweise in der Geschichte der Solenomyiden und Nuculaceen. *Geologische und Paleontologische Abhandlungen*, vol. 22 (new ser. vol. 18):1-119 p.

Runnegar, B. N. 1983. Molluscan phylogeny revisited. *Memoirs of the Association of Australasian Palaeontologists* 1:121-144.

Runnegar, B. N. 1985. Shell microstructures of Cambrian molluscs replicated by phosphate. *Alcheringa* 9:245-257.

Runnegar, B. N. 1996. Early evolution of the Mollusca: the fossil record.

In: Origin and Evolutionary Radiation of the Mollusca, J. Taylor, ed. pp. 77-87. Oxford University Press, Oxford.

Runnegar, B. N. and J. Pojeta, Jr. 1974. Molluscan phylogeny: the paleontological viewpoint. *Science* 186:311-317.

Runnegar, B. N. and P. A. Jell. 1976. Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. *Alcheringa* 1:109-138.

Runnegar, B. N. and C. Bentley. 1983. Anatomy, ecology and affinities of the Australian early Cambrian bivalve *Pojetaia runnegari* Jell. *Journal of Paleontology* 57(1):73-92.

Runnegar, B. N. and J. Pojeta, Jr. 1985. Origin and diversification of the Mollusca. *In: The Mollusca, Volume 10, Evolution*. E. R. Trueman and M. R. Clarke, eds. pp. 1-57. Academic Press, Inc., Orlando.

Runnegar, B. N. and J. Pojeta, Jr. 1992. The earliest bivalves and their Ordovician descendants. *American Malacological Bulletin* 9(2):117-122.

Salter, J. W. 1852. Note on the fossils above mentioned from the Ottawa River. *British Association for the Advancement of Science, 21st Meeting, 1851, Notices and Abstracts, etc.*, pp. 63-65.

Sandberg, P. A. and J. D. Hudson. 1983. Aragonite relic preservation in Jurassic calcite-replaced bivalves. *Sedimentology* 30:879-892.

Sanders, H. L. and J. A. Allen. 1973. Studies on deep-sea Protobranchia (Bivalvia); prologue and the Pristiglomidae. *Bulletin of the Museum of Comparative Zoology* 145: 237-362.

Say, T. 1822. An account of some of the marine shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2:221-248; 257-276; 302-325.

Scarlato, O. A. and Y. I. Starobogatov. 1979. General evolutionary patterns and the system of the class Bivalvia. *Trudy Zoologicheskogo Instituta, Akademiya Nauk, SSSR*, 80, 5-38. [In Russian]. See English translation by K. J. Boss, and M. K. Jacobson, 1985, Special Occasional Publication No. 5, Department of Mollusks, Harvard University, Cambridge, Massachusetts, 67 pp.

Schenck, H. G. 1934. The classification of nuculid pelecypods. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 10:1-78.

Schenck, H. G. 1944. *Lamellinucula*, a new subgenus of the nuculid pelecypods. *Journal of Paleontology* 18(1):97-99.

Schmidt, W. J. 1922. Über der Aufbau der Schale von *Nucula*. *Archiv für Mikroskopische Anatomie* 96:171-181.

Sharpe, D. 1853. Descriptions of the new species of Zoophyta and Mollusca. *In:* On the Carboniferous and Silurian Formations in the neighborhood of Bussaco in Portugal, C. Ribeiro, D. Sharpe, and T. R. Jones. *Quarterly Journal of the Geological Society of London* 9:146-158, pls. 7-9.

Soot-Ryen, H. 1964. Nuculoid pelecypods from the Silurian of Gotland. *Arkiv för Mineralogi, Svenska Vetenskaps-Akademien* 3(28):489-519.

Speden, I. G. 1970. The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota. Part 2. Systematics of the Bivalvia. *Yale University Peabody Museum Bulletin* 33:1-222, 42 pls.

Suzuki, S. 1983. Reexamination of the composite prismatic structure in bivalve shell. *Bulletin of the Fukuoka University of Education* 32(3):811-841.

Taylor, J. D. 1973. The structural evolution of the bivalve shell. *Palaeontology* 16:519-534.

Taylor, J. D., W. J. Kennedy, and A. Hall. 1969. The shell structure and mineralogy of the Bivalvia. Introduction. Nuculacea - Trigonacea. *Bulletin of the British Museum (Natural History), Zoology*, Supplement 3:1-125, 29 pls.

Thiele, J. 1931-1935. *Handbuch der Systematischen Weichtierkunde*, Vol. 1, 1931, p. 1-778; Vol. 2, 1935, p. 779-1154. Gustav Fischer (Jena).

Trueman, E. R. 1952. Observations on the ligament of *Nucula*. *Proceedings of the Malacological Society of London* 29(5):201-205.

Ulrich, E. O. 1894. The Lower Silurian Lamellibranchiata of Minnesota. From Vol. 3 of the *Final Report of the Geological and Natural History Survey of Minnesota*, p. 475-628 (Published and distributed under separate cover prior to the entire volume 3).

Van de Poel, L. 1955. Structure du test et classification des nucules. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique* 31(3):1-11.

Vostokova, V. A. 1962. Kembriyskiy gastropody Sibirskoy Platformy i Taymyra. [Cambrian gastropods from the Siberian Platform and Taymyr]. *In:* Statei po Paleontologii i Biostratigrafii, 28, *Nauchno-Issled. Inst. Geol. Arktiki, Sbornik*, 28:51-74. [In Russian]

Waller, T. R. 1990. The evolution of ligament systems in the Bivalvia. *In: The Bivalvia - Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh, 1986*, B. Morton, ed. pp. 47-91. Hong Kong University Press, Hong Kong.

Waller, T. R. 1998. Origin of the molluscan class Bivalvia and a phylogeny of major groups. *In: Bivalves: an Eon of Evolution - Paleobiological Studies Honoring Norman D. Newell*. P. A. Johnston and J. W. Haggart, eds. University of Calgary Press, Calgary, 1-45.

Williams, H. S. and C. L. Breger. 1916. The fauna of the Chapman Sandstone of Maine including descriptions of some related species from the Moose River Sandstone. *U. S. Geological Survey Professional Paper* 89:1-347, 27 pls.

Wise, S. W., Jr. 1970. Microarchitecture and mode of formation of nacre (mother of pearl) in pelecypods, gastropods, and cephalopods. *Eclogae Geologicae Helvetiae* 63:775-797.

Wöhrmann, S. F. von. 1893. Ueber die Systematische Stellung der Trigoniden und die Abstammung der Nayaden. *K. K. Geologische Reichsanstalt Wien, Jahrbuch*, no. 43(1893):1-28.

Wrigley, A. 1946. Observations on the structure of lamellibranch shells. *Proceedings of the Malacological Society of London* 27(1):7-19.